STUDIES ON FRESHWATER PHYTOPLANKTON

with special reference to the Desmidiaceae.

Thesis submitted for the Degree of Doctor of Science

in the University of Edinburgh,

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Published papers:-

(1) A systematic account of the phytoplankton of the Blue and White Nile. Ann. Mag. Nat. Hist. Ser. 12, vol. 7, 1954, 648-656.

(2) The influence of the Gebel Aulyia Dam on the development of Nile plankton. J. Animal Ecol., 23, 1954, 101-114. (with J. Rzoska).

(3) Seasonal plankton development in the White and Blue Nile near Khartoum. Verh. int. Ver. Limnol., 12, 1955, 327-334. (with J. Rzoska, and G.A. Prowse).

(4) On the ecology of the terrestrial alga, Fritschiella tuberosa, in the Sudan. New Phytol., 55, 1956, 130-132.

(5) A bibliography of African freshwater algae. Rev. Algol. 4, 1957, 207-238. (with Ross, Kufferath & Sims).

(6) Some observations on the effects of water inflow and outflow on the plankton of small lakes. J. Animal Ecol., 25, 1956, 22-35. (with W.B. Woodward).

(7) Fertilization experiments on Scottish freshwater lochs. I. Loch Kinardochy. Sci. Invest. Freshwat. Fish. Scot. 17, 1957, 30 pp. (with A.V. Holden).

(8) Changes in the phytoplankton of some Scottish hill lochs resulting from their artificial enrichment. Verh. internat. Ver. Limnol. XIII, 1958, 298-305.

(9) The aquatic fauna as an ecological factor in studies of the occurrence of freshwater algae. Rev. algol., (N.W.) 1, 1955, 141-145.

(10) Notes on some uncommon algae from lochs in the Tummel-Garry catchment area. Trans. bot. Soc. Edinb., 36 (3), 1954, 207-214.

(11) Notes on some uncommon algae from lochs in Kinross, Perthshire and Caithness. Trans. bot. Soc. Edinb., 36, 1955, 309-16.

(12) Notes on freshwater algae, mainly from lochs in Perthshire and Sutherland, Trans. bot. Soc. Edinb., 37, 1957, 114-122.

(13) Notes on algae from the plankton of some Scottish freshwater lochs. Trans. bot. Soc. Edinb., 37 (3), 1958, 174-181.

(14) On some forms of Micrasterias new to or rare in Britain. Naturalist, Lond., April-June, 1957, 37-39.

(15) The status of desmids in the phytoplankton and the determination of phytoplankton quotients. J. Ecol., 47, 1959, 429-445.

(16) The phytoplankton of some Irish loughs and an assessment of their trophic status. Proc. Roy. Irish Acad., 60 B. (4), 1959, 167-191. (with F.E. Round).

(17) Notes on desmids of the genus Staurastrum III. S. paradoxum Meyen in the Jenner Herbarium of the British Museum. Naturalist Lond., July-Sept. 1959, 81-83.

(18) The published figures of the desmid Staurastrum paradoxum. Rev. Algol. 4, 1959, 239-255.

(19) Staurastrum paradoxum Meyen and S. gracile Ralfs in the British freshwater plankton, and a revision of the S. anatinum - group of radiate desmids. Trans. Roy. Soc. Edinb. LXIII No. 26, 1959, 589-628.

(20) De Brebisson's determinations of Staurastrum paradoxum Meyen and S. gracile Ralfs. Nova Hedwigia, 1(2), 1959, 163-166.

(21) The varieties of Staurastrum paradoxum Meyen - nomen dubium. Nova Hedwigia, 1(4), 1960, 431-442.

(22) Notes on desmids of the genus Staurastrum I. S. pseudopelagicum, S. subcruciatum, S. avicula and S. denticulatum. Naturalist, Lond., July-Sept. 1957, 97-100.

(23) Notes on desmids of the genus Staurastrum. II. S. leptodermum, S. longispinum, S. brasiliense, S. setigerum, S. clevei and S. tohopekaligense var. trifurcata. Naturalist, Lond. July-Sept. 1958, 91-95.

(24) Staurastrum pendulum var. pinguiforme Croasdale. S. micron, West, f. major f. nov., fac. quadrata and S. micron var. perpendiculatum (Cronblad) nov. comb., desmids new to the British freshwater plankton. Nova Hedwigia, 1(2), 157-162.

(25) Desmids from the plankton of some Irish loughs. Proc. Royl. Irish Acad. 59 B (6), 1958, 71-91.

FORWARD

The papers submitted herewith relate to personal researches on various aspects of the biology of phytoplankton principally in Scottish freshwater lochs but also of the river plankton in the White and Blue Niles in the Sudan. The latter studies were conducted as part of a programme of work on the fundamental hydrobiology of the Nile initiated by Dr. J. Rzoska and the author, who together inaugurated the Nile Hydrobiological Research Unit. An introduction to this work is the systematic account of the algal plankton of both rivers (1) and is based on collections made between 1949 and 1952 from the Blue Nile at Khartoum and from many places between Khartoum and the Sudd region on the White Nile. Some of the effects, on the river's plankton and hydro-chemistry, of impounding water above the Gebel Aulyia Dam on the White Nile, south of Khartoum, were studied by taking a succession of samples from the Dam upstream for 325 Km (2). It was found that the plankton showed a numerical increase of more than 100-fold, the increase being associated with the change from river-to lake-like conditions as the Dam was approached. The seasonal development of the plankton in the White and Blue Nile has also been investigated (3). This study was based on regular samples collected over a period of three years, from 1951-53, and indicates that although regular annual fluctuations in plankton density occur in both rivers, their peaks do not coincide but

show a marked dependance on the specific hydrological regimes of the two rivers, which are briefly summarised. Related to these studies on Nile algae are some observations on the ecology of the terrestrial alga, Fritschiella tuberosa which makes a seasonal appearance on drying mud on the banks of the Blue Nile (4). Some details of the exacting environmental conditions under which this alga grows are presented. A comprehensive survey and bibliography of the literature relating to the freshwater algae of Africa has also been compiled (5).

The papers on the phytoplankton of Scottish freshwater lochs have been assigned to three categories. These relate to studies:-

I. On water replacement in relation to plankton productivity (6). Here it has been shown that water inflow and outflow in small lakes may be a factor of over-riding importance in determining the abundance of plankton. This study is related to the observations made on the White Nile plankton at the Jebel Aulyia Dam (2).

II. On the effects on the phytoplankton of adding mineral fertilizers to hill lochs (7 & 8). These studies which are contributions towards investigations of the factors affecting the biological productivity of Scottish freshwaters, show that quite small additions of phosphate produce quite profound and prolonged effects on the phytoplankton of the treated lochs. Also bearing on this work are observations

made on the aquatic fauna as an ecological factor in studies of the occurrence of freshwater algae (9).

During the course of all these investigations the phytoplankton of many lochs were examined and observations made on this somewhat neglected aspect of Scottish vegetation. These have been published in a series of short papers (10-14).

III. On the desmid-plankton which is especially prominent in many Scottish lochs (15-25). This aspect of phytoplankton research was begun in an attempt to use plankton algae as indications of the trophic status of lakes (15 & 16). It was found, however, that the taxonomy of the most commonly occurring genus, Staurastrum, was so confused that before any real progress could be achieved a detailed reinvestigation would have to be made of many of the supposedly well established, commonly occurring species. Most prominent amongst these were S. paradoxum and S. gracile, species which, according to the literature are amongst the most widespread of plankton organisms not only in the British Isles and Europe, but throughout the world. An attempt has therefore been made to rationalize the taxonomy of these two supposedly cosmopolitan species (17 - 21). Studies have also been

made on other desmids from the British freshwater plankton again with special reference to the genus Staurastrum (22 - 25).

From the ANNALS AND MAGAZINE OF NATURAL HISTORY
Ser. 12, vol. vii, p. 648, *September*, 1954.

A SYSTEMATIC ACCOUNT OF THE PHYTOPLANKTON OF THE BLUE AND WHITE NILE.

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During the past 50 years several papers have been published concerning the phytoplankton of various regions of the River Nile. These, however, all relate to collections made either at the source of the White Nile, in Lake Victoria (Schmidle 1902, West 1907, Ostenfeld 1908, 1909, Woloszynska 1914, Bachmann 1933), or in the lower reaches of the main river in Egypt (Kaufmann 1897, Brunnthaler 1914, Abdin 1948). The present account is based on collections made in the Sudan between 1949 and 1952, from the Blue Nile at Khartoum (no part of this important tributary has been previously studied), and from many places between Khartoum and the Sudd region on the White Nile.

Quantitative studies (Brook & Rzóska 1950/1954, Rzóska, Brook & Prowse—in the press) have indicated that when fully developed the phytoplankton of both the Blue and White Nile is like that of a typical eutrophic lake being composed principally of blue-green algæ and diatoms, though at times net hauls may contain a conspicuous assemblage of Chlorococcales, of which *Pediastrum* species are most abundant. These studies have shown that the abundance of the plankton is inversely proportional to the current speed of the river which in various places, at certain times of the year, is impeded by dams. Regular annual fluctuations in plankton density occur in both rivers, the most productive period in the White Nile being between October and December, and in the Blue Nile from January to June. For a considerable period of each year, usually between July and September, both rivers are almost devoid of plankton.

In the following account the abbreviations B.N. and W.N. have been used to denote Blue and White Nile respectively. The Roman numerals indicate the months during which the species in question have been found.

CHLOROPHYCEAE.

Volvocales.

Chlamydomonadaceae.

Chlamydomonas sp. Occasionally individuals of this genus have been observed in samples from B. & W.N. but these have been in preserved material, thus not admitting specific determination. However, from

temporary pools formed as the levels of both tributaries fall, the following species of *Chlamydomonas* have been identified :—

C. attenuata Pascher.
C. ehrenbergii Gorosch.
C. microscopica G. S. West.
C. subasymetrica Pascher.
C. subcaudata Wille.

Thus it is believed that these species may be present from time to time in the plankton.

Gonium sociale (Duj.) Warming. Rare B.N. I–V.

G. pectorale O. F. Muell. Rare B.N. I–V.

Pandorina morum (O. F. Muell) Bory. Occ. B.N. I–V. Occ. W.N. XI–V. Most frequent in lagoons and backwaters of W.N. in Sudd region.

Eudorina elegans Ehrenb. Similar distribution and occurrence to *Pandorina*.

Eudorina sp. (near *E. illinoisensis* Pascher in Sussw. Fl. Mitteleur. **4**, 1927, p. 443, figs. 404–5). One colony from W.N. XII. Colony 140 × 120 μ. Four small vegetative cells each 10 μ diam. and 28 reproductive cells 14 μ diam. Chloroplasts distinctly lobed as in *E. illinoiensis*.

Volvox aureus Ehrenb. Periodically freq. W.N. I–VI. Occ. B.N. I–VI.

V. globator (L.) Ehrenb. Freq. B.N. III & IV. Present on occasions with *V. aureus* in W.N.

Palmellaceae.

Sphaerocystis schroeteri Chodat. Occ. W.N. XI–III. Not previously recorded from the Nile Basin.

Asterococcus limneticus G. M. Smith in Bull. Wisc. Geol. & Nat. Hist. Survey, **57** : p. 104, 1920. V. rare W.N. XII. Colonies 160 μ diam., with 16 cells per colony, each cell 18 μ diam. A new record for Africa.

Gloeocystis gigas (Kütz.) Lagerh. Though not found in the main stream, this alga has been found on several occasions in lagoons and khors adjoining W.N. in the Sudd region.

CHLOROCOCCALES.

Hydrodictyaceae.

Pediastrum boryanum (Turp.) Menegh. Occ. B.N. & W.N. XI–V.

P. boryanum var. *granulatum* (Kütz.) A. Braun. V. rare B.N. III–V.

P. boryanum var. *longicorne* Reinsch. Rare B.N. III–V.

P. duplex Meyen. Occ. W.N. XI–III : B.N. I–VI.

P. duplex var. *gracillimum* W. & G. S. West. Rare B.N. I–VI.

P. duplex var. *reticulatum* Lagerh. Freq. W.N. XI–II : B.N. I–VI.

P. clathratum (Schroeter) Lemm. Comm. B.N. II–VI. Freq. W.N. X–II.

P. simplex var. *duodenarum* (J. W. Bailey) Rabenh. Occ. B.N. III–V.

P. simplex var. *radians* Lemm. Rare B.N. III–V.

P. sturmii Reinsch. Rare B.N. II–V.

P. tetras (Ehrenb.) Ralfs. Rare W.N. X–IV : B.N. I–V.

Sorastrum americanum (Bohlin) Schmidle. Rare B.N. III–V : also in lagoons and khors adjoining W.N., though never found in main stream.

Chlorellaceae.

Micratinium radiatum (Chodat) Wille. V. rare B.N. II–VI.

M. pusillum Fresen. Common W.N. X–XII (max. usually XI). Occ. B.N. I–V.

Oocystaceae.

Oocystis borgei Snow (see Rich, Trans. Roy. Soc. S. Africa **20**, 1932, p. 160–1, fig. 3 *a-e*). Occ. W.N. X–III.

O. elliptica W. West. V. rare B.N. V.

Nephrocytium lunatum G. S. West. Occ. W.N. X–V.

N. agardhianum Naeg. V. rare in plankton of a lagoon near Ed Dueim, W.N. Not found in main stream.

Tetraedron bifurcatum (Wille) Lagerh. Rare W.N. XI.

T. enorme (Ralfs) Hansg. Rare B.N. II–V.

T. limneticum Borge. Rare B.N. I–V.

T. minimum (A. Braun) Hansg. Occ. B.N. I–V. Rare W.N. X–XII.

T. proteiforme (Turn.) Brunnth. V. rare W.N. X & XI.

T. planktonicum G. M. Smith. V. rare W.N. XI.

T. regulare Kütz. Rare B.N. III–V.

T. tetragonum (Naeg.) Hansg. with the forma *arthrodesmiforme* G. S. West (see West, J. Bot. **67**, 1909, p. 245, pl. 498, fig. 1). Occ. W.N. X–I. Rare B.N. III–V.

T. victoriae Wolosz. Rare B.N. III–VI. Cells mostly 30 $\mu \times 20\ \mu$.

T. trigonum (Naeg.) Hansg. Rare W.N. XI–XII.

Polyedriopsis quadrispina G. M. Smith in Bull. Wisc. Geol. & Nat. Hist. Survey, **57**, 1920. Occ. B.N. V–VI. Cells 8 μ broad, quadrate, with a single stout seta at each angle and set in one plane at right-angles to one another. Setæ 3 μ broad at their base, tapering to a fine point; up to 40 μ in length.

Selenstraceae.

Ankistrodesmus falcatus (Corda) Ralfs. Occ. W.N. XI–V : B.N. I–VI.

A. falcatus var. *acicularis* (A. Braun) G. S. West. Rare B.N. XII–V.

A. falcatus var. *duplex* (Kütz) G. S. West. Occ. W.N. XII.

A. falcatus var. *spirilliformis* G. S. West. Occ. B.N. XII–VI.

Schroederia setigera (Schröder) G. M. Sm. V rare. W.N. X–IV. V. occ. B.N. III–VI.

Actinastrum hantzschii Lagerh. var. *intermedium* Teiling. Occ. W.N. X–V. Cells mostly 18–23 μ long × 2–2·5 μ broad, and slightly crescent-shaped.

A. schroeteri G. Huber. Occ. B.N. XII–VI. Cells 12–15 μ long × 2 μ broad, free ends drawn out to fine points.

Selenastrum capricornicum Printz. V. rare W.N. X–XII. Cells 10 μ long × 2 μ broad. Not previously recorded from Africa.

S. gracile Reinsch. Occ. B.N. I–VI.

Kirchneriella lunaris (Kirchn.) Moeb. Rare W.N. X–V.

K. obesa W. & G. S. West. Occ. W.N. X–IV. Both species of *Kirchneriella* are more abundant in lagoons and backwaters of the river.

Dictyosphaeriaceae.

Dictyosphaerium pulchellum H. C. Wood. Freq. W.N. XI–II. Occ. B.N. I–VI.

Westella botryoides De Wild. Freq. W.N. X–II. Occ. B.N. I–VI.

In many of the B.N. colonies the cells are markedly flattened on their inner faces and the groups of four cells arranged in a linear series (see Rich 1932, Trans. Roy. Soc. S. Africa, **20**, pt. 2, p. 163 and fig. 48).

Dimorphococcus lunatus A. Braun. Rare W.N. X–III and B.N. II–V. Finest specimens present in plankton of lagoons adjoining White Nile.

Coelastraceae.

Crucigenia quadrata Morren. Rare B.N. II–VI and W.N. XI–III.

Crucigenia rectangularis (A. Braun) Gay. Rare B.N. III–VI.

Scenedesmus acuminatus (Lagerh.) Chodat. Occ. B.N. I–V. V. rare W.N. X–II.

S. bijugatus (Turp.) Lagerh. Occ. B.N. XII–VI: W.N. X–III. Forms approaching the var. *alternans* Hansg. are quite common.

S. obliquus (Turp.) Kütz. Occ. B.N. XII–IV.

S. opoliensis Richter. Rare B.N. III–VI. V. rare W.N. XI–XII.

S. quadricauda (Turp.) Bréb. Occ. B.N. XII–VI. Rare W.N. X–III.

Coelastrum cambricum Archer. Rare B.N. I–V. V. rare W.N. X–I.

C. microporum Naeg. Rare B.N. II–VI. Rare W.N. XI–III.

C. proboscideum Bohlin. V. rare B.N. I–IV.

C. reticulatum (Dang.) Senn. Occ. B.N. III–VI. Freq. W.N. X–I.

C. sphaericum Naeg. Occ. B.N. II–VI. W.N. X–I.

Tetrastrum heterocanthum (Nordst.) Chodat. V. rare B.N. III.

CONJUGALES.

Zygnemaceae.

Spirogyra spp. Occ. filaments of several species of this genus are found particularly in the more southerly stretches of the White Nile towards the Sudd region. *S. africana* (Fritsch) Czurda occurs most frequently.

Mougeotia spp. Freq. in W.N., particularly in plankton of lagoons in regions of the river south of Kosti. Material with zygotes has been found in W.N. and identified as *M. scalaris* Hass. and *M. capucina* (Bory.) Agardh. Occ. in B.N. II–VI. *M. tenuissima* (De Bary) Czurda and *M. viridis* (Kutz.) Wittr. have been identified.

Gonatozygaceae.

Gonatozygon aculeatum Hastings. Occ. W.N. XI–I.

G. monotaenium De Bary. V. rare W.N. X : B.N. II and III.

Desmidiaceae.

CLOSTERIOIDEAE.

Closterium acutum Bréb. Rare B.N. III–VI.

C. acutum var. *variabile* Krieger. Occ. B.N. III–VI. V. rare W.N. X–XII.

C. lanceolatum Kütz. Occ. B.N. I–V.

C. leibleinii Kütz. Occ. B.N. XII–IV.

C. lineatum Ehrenb. Occ. B.N. II–V. Rare W.N. X–I.

C. parvulum Naeg. var. *angustum* W. and G. S. West. A few individuals found in plankton of lagoons adjoining W.N. in Sudd region.

C. setaceum Ehrenb. Rare W.N. X–II, though freq. in plankton in lagoons near Sudd.

C. strigosum Bréb. V. rare W.N. XII.

C. substrigosum W. & G. S. West in Ann. Roy. Bot. Gard. Calcutta, **6**, 1907, p. 192, pl. xiii, fig. 19. V. rare W.N. XII. Cells mostly 230 $\mu \times 7$ μ.

COSMARIOIDEAE.

Euastrum spinulosum Delp. subsp. *africanum* Nordst. Occ. W.N. X–III. Rare B.N. II–V.

E. divergens Joshua. V. rare W.N. XII.

Micrasterias tropica Nordst. V. rare W.N. XII.

M. crux-melitensis (Ehrenb.) Hass. V. rare W.N. XII.

Cosmarium botrytis (Bory) Menegh. Occ. W.N. X–III : B.N. I–VI.

C. laeve Rabenh. Freq. W.N. XII–II.

C. moniliforme (Turp.) Ralfs. Occ. B.N. II–VI. V. rare W.N. XII–I.

C. subtumidum Nordst. var. *klebsii* (Gutw.) W. & G. S. West. V. rare W.N. XII.

C. blytii Wille var. *novae-sylvae* W. & G. S. West. Rare W.N. X–II.

Arthrodesmus convergens Ehrenb. V. rare W.N. X–II.

A. subulatus Kütz. V. rare W.N. XII.

Staurastrum gracile Ralfs. Rare W.N. X–III : B.N. II–V. An individual approaching the var. *nyansae* West found in lagoon adjoining W.N.

S. leptocladum Norst forma *africanum* G. S. West. Occ. W.N. X–III.

S. limneticum Schmidle. Occ. W.N. XII–IV : B.N. III–VI.

S. volans W. & G. S. West. V. rare W.N. XII–I.

HETEROKONTAE.

Heterochloridales.

Centritractus belonophorus Lemm. V. rare W.N. XII.

Stipitococcus urceolatus W. & G. S. West. Freq. as epiplankter on *Melosira granulata* in W.N.

Heterococcales.

Ophiocytiaceae.

Ophiocytium capitatum Wolle var. *longispinum* Lemm. Rare B.N. II–IV.

O. capitatum var. *longispinum* Lemm. Rare W.N. XII.

O. cochleare A. Braun. V. rare B.N. III.

BACILLARIOPHYCEAE.

Centrales.

Coscinodiscaceae.

Melosira agassizii Ostenf. Freq. W.N. X–IV : B.N. XII–VI.

M. agassizii var. *malayensis* Hust. Occ. with type-sp. in W.N. & B.N. A new African record.

M. ambigua (Grun.) O. F. Müll. Rare W.N. X–I.

M. granulata (Ehrenb.) Ralfs. Dominant W.N. IX–XI & II–V. Dominant B.N. XI–XII & V–VI.

M. granulata var. *angustissima* O. F. Müll. Common at times with type sp. in both rivers. The f. *spiralis* has been found on rare occasions in W.N.

M. granulata var. *valida* Hust. Rare W.N. XII.

M. nyassensis var. *victoriae* O. F. Müll. Rare W.N. XI–I.

M. varians C. A. Ag. Occ. W.N. XI–II. Rare B.N. II–V.

Cyclotella comta (Ehrenb.) Kütz. Rare W.N. XI–III.

C. meneghiniana Kütz. Rare W.N. XI–III. Occ. B.N. II–V.

C. kutzingiana Chauvin. Occ. W.N. X–II.

PENNALES.

Fragilariaceae.

Synedra acus Kütz. Rare W.N. X–II.

S. acus var. *radians* (Kütz) Hust. Freq. W.N. X–I. Occ. B.N. XII–V.

S. cunningtonii G. S. West. Occ. W.N. XI–I.

S. nyansae G. S. West. V. rare W.N. XII.

S. ulna (Nitzsch.) Ehrenb. Occ. W.N. XI–IV : B.N. II–VI.

S. ulna var. *spathulifera* Grun. Occ. W.N. XI–II. All the forms of this var. as illustrated in Huber-Pestalozzi (1942), taf. cxxxv, fig. 543 a-g, have been found.

Nitzschiaceae.

Nitzschia acicularis (Kütz.) W. Sm. Common W.N. XI–I : B.N. XII–I.

N. lanceolata W. Sm. V. rare W.N. XII.

N. nyassensis O. F. Müll. V. rare W.N. XII.

N. palea (Kütz.) W. Sm. Occ. W.N. XI–IV : B.N. XII–V.

Family **Surirellaceae.**

Surirella linearis W. Sm. Rare W.N. XI–I : B.N. III–VI.

Cymatopleura elliptica (Bréb.) W. Sm. V. rare W.N. XII.

EUGLENOPHYCEAE.

Euglena granulata (Klebs) Lemm. Rare B.N. II–V.

Phacus pleuronectes (O. F. Müll.) Duj. Rare W.N. XI–III. V. rare B.N. III–VI.

P. longicauda (Ehrenb.) Duj. V. rare W.N. XII ; more abundant in lagoons.

CYANOPHYCEAE (MYXOPHYCEAE).

CHROOCOCCALES.

Chroococcaceae.

Microcystis aeruginosa Kütz. Freq. W.N. XII–I. Occ. B.N. I–III.

M. flos-aquae (Wittr.) Kirchn. Comm. W.N. XI–I, sometimes producing water-blooms on the Gebel Auylia Dam and in lagoons in Sudd region. Freq. B.N. I–III. In both tributaries this alga is often found with the epiplankter *Phormidium mucicola*.

M. pulvera var. *incerta* (Lemm.) Crow. Occ. W.N. XI–I.

Aphanocapsa delicatissima W. & G. S. West. Freq. W.N. XI–II.

A. koordersi Strom. Rare B.N. I–IV.

Chroococcus limneticus Lemm. Freq. W.N. X–XII.

C. limneticus var. *subsalsus* Lemm. Rare B.N. IV–VI.

Chroococcus dispersus var. *minor* G. M. Sm. V. rare W.N. XII.

C. turgidus (Kütz.) Naeg. Rare W.N. X–II : B.N. XII–V.

Gomphosphaeria lacustris Chodat. V. rare B.N. I–III.

Merismopedia glauca (Ehrenb.) Naeg. V. rare W.N. X–I.

M. minima Beck. Rare B.N. XII–IV.

M. punctata Meyen. Rare B.N. XII–IV.

M. tenuissima Lemm. Occ. B.N. II–IV.

HORMOGONALES.

Raphidiopsis curvata Fritsch. Common W.N. XI–I. Freq. B.N. I–IV. Although first described from standing water in South Africa, this species, which at times forms an important constituent of the plankton of both tributaries, has not been recorded from any other part of Africa.

R. mediterranea Skuja. Occ. B.N. V & VI. Not previously recorded from Africa.

This is thought be identical with *Aphanizomenon kaufmanii* Schmidle (=*Cylindrospermum*? *kaufmanii* (Schmidle) Huber-Pest., which is recorded from the Nile at Cairo by Kaufmann in his paper "Sur le pretendu du Nil vert". See Huber-Pestalozzi (1938) p. 180 and fig. 74 A, and p. 191 and fig. 89.

Anabaenopsis cunningtonii W. R. Taylor. Comm. W.N. XI & XII.

Anabaenopsis circularis (G. S. West) Wolosz. & Miller. Occ. B.N. I–IV.

A. tanganyikae (G. S. West) Wolosz. & Miller. Freq. W.N. X–I : B.N. II–V.

Nodularia spumigena Mertens. Rare W.N. XII : B.N. XII–III. A few filaments have been seen in B.N. of the var. *major* Born. & Flah. with cells 14–17 μ broad.

Anabaena aphanizomenoides Forti. Occ. W.N. X–XII. Trichomes 3·5 μ broad × 4–8 μ long, with gas vacuoles ; heterocysts 4 μ broad × 5 μ long; spores sphærical, mostly 8 μ diam.

A. catenula Born. & Flah. Occ. B.N. XII–IV.

A. constricta (Szafer) Geitler. Occ. B.N. I–III.

A. flos-aquae Born. & Flah. var. *intermedia* f. *spiroides* Woron. Dominant W.N. XI–I : B.N. I–IV., often causing water blooms. On occasions the trichomes of this alga become coiled to form compact discs of up to 40 μ in diam. These discs closely resemble the form *discoidea* of *A. flos-aquae* described by Schmidle (1902) from L. Nyassa and renamed *A. discoidea* by Ostenfeld (1908).

A. inaequalis Born. & Flah. Occ. B.N. I–III.

A. scheremetievi Elenk.? Rare B.N. I–IV. Cells 8 μ × 8 μ broad; heterocysts 10 μ broad × 9 μ long; spores not observed.

Spirulina major Kütz. Rare B.N. II–V.

S. subtilissima Kütz. V. rare W.N. XI–II.

Oscillatoria agardhii var. *isothrix* Skuja. Occ. W.N. X–XII. Trichomes straight, except for slight curving at tips which are slightly attenuated, 8–10 μ broad; cells 2–4 μ long, trichomes up to 300 μ long.

O. geminata Gom. Freq. W.N. X–I.

O. limnetica Lemm. V. rare W.N. XII.

O. planktonica Wolos. Occ. W.N. X–I.

O. princeps Vauch. V. rare W.N. XII, though frequent in plankton of lagoons towards Sudd region.

Phormidium mucicola Naumann & Huber-Pest. Freq. in both tributaries as epiplankter on *Microcystis flos-aquae* and *Aphanocapsa pulchra*.

Lynbgya limnetica Lemm. Dominant W.N. XI & XII. Rare B.N. I–III.

BACTERIA.

Eubacteria.

Chlamydobacteriaceae.

Crenothrix polyspora Cohn. Occ. W.N. XII, and freq. in plankton of lagoons in Sudd region.

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THE INFLUENCE OF THE GEBEL AULYIA DAM ON THE DEVELOPMENT OF NILE PLANKTON

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(With 3 Figures in the Text)

INTRODUCTION

Although the hydrology of the Nile has been thoroughly investigated by the Egyptian and the Sudan Irrigation Departments, the only detailed biological work published to date is on the algal flora of the lower reaches (Abdin 1946, 1947, 1948, 1949). During the past few years investigations on the middle and upper reaches have, however, been started by biologists from the University College, Khartoum.

The hydrological and, apparently, also the biological conditions of the river have been altered profoundly by man, and further considerable changes are yet to be made. The dams at Sennar (Blue Nile), Gebel Aulyia (White Nile) and Aswan (Lower Nile), in addition to the natural barriers, the cataracts and swamps, divide the river into regions, distinctive not only in their utilitarian and geographical aspects, but also showing specific biological features. The distances of 5611 km. from the Delta to Lake Victoria on the White Nile and the 4590 km. to Lake Tana at the head of the Blue Nile, render a biological survey of the river an immense task, and thus investigations must be carried out in sectors defined by natural conditions and transport limitations. One such sector is on the White Nile south of Khartoum (Fig. 1), where the Gebel Aulyia Dam converts the river into a shallow, slow-flowing 'lake', which in places is three miles broad. The dam, built in 1937 44 km. south of Khartoum, provides an irrigation reservoir for Egypt. Each July the dam is closed and the reservoir begins to store water; when full, normally by September, it holds $3{\cdot}5 \times 10^9$ cu.m. As a result, a rise in river level is recorded more than 500 km. upstream of the dam. Not until February is the dam fully opened to allow for the decreasing flow in the Blue Nile, and the water in the reservoir shrinks to normal river level by May. Strong southerly or northerly winds, according to the season, frequently produce impressive waves on this vast, open, temporary 'lake'.

The present paper examines the effects of the storage of this large volume of water on plankton production in part of the river upstream of the dam. A series of samples were taken from a place near Khartoum to beyond Gebelein, a distance of 396 km., samples and data being collected at eleven stations, separated by distances varying from 20 to 70 km. (Fig. 1). The river journey was completed between 13 and 18 December 1951, thus ensuring a reasonable comparability of samples in time, an important consideration in flowing water.

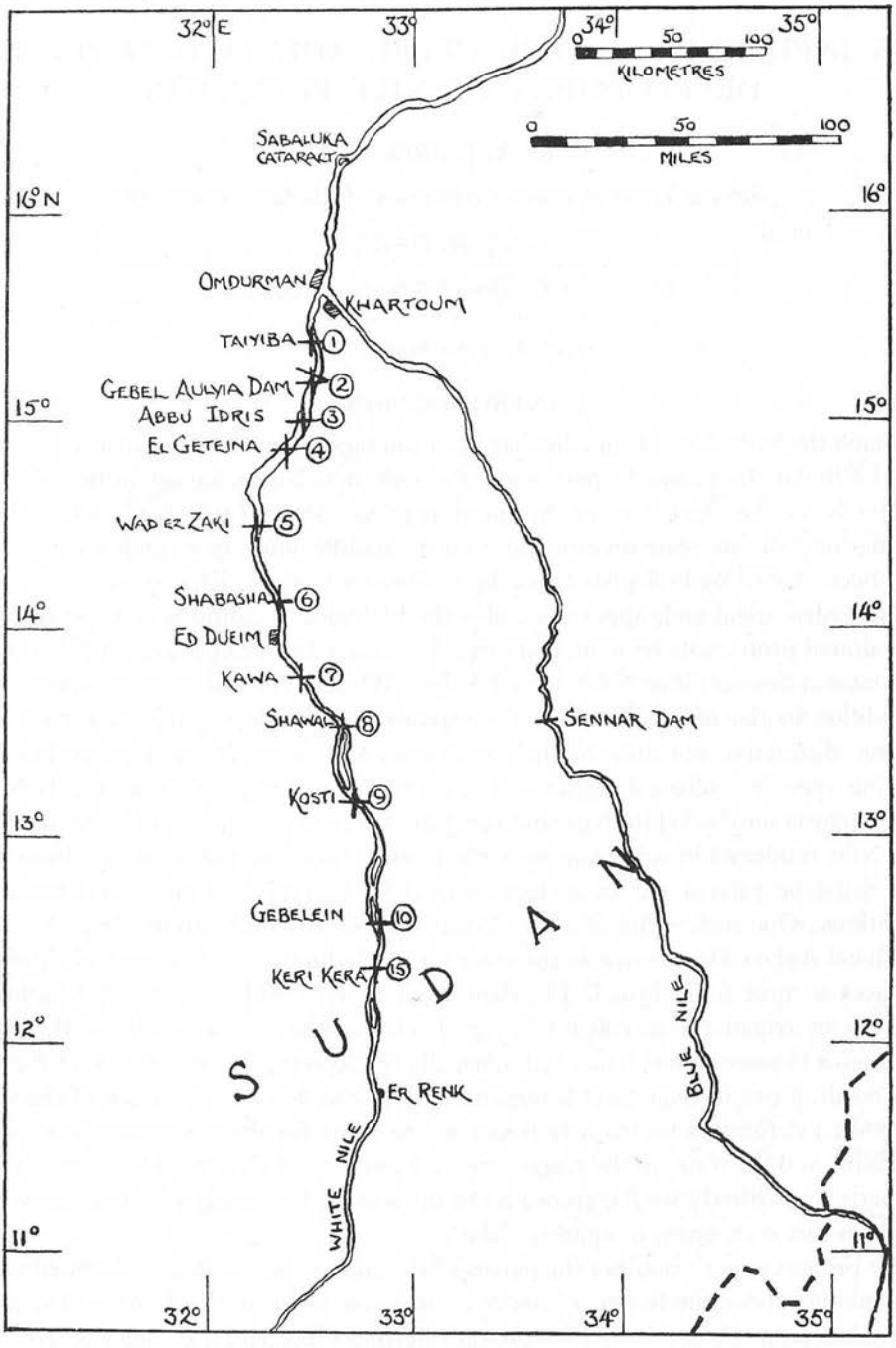

Fig. 1. Map of part of the White Nile showing sampling stations.

METHODS

Quantitative water samples were taken with a Friedinger sampler of 2 l. capacity. At each station, duplicate samples from three levels (surface, middle and bottom) were obtained except where the river was very shallow, when only surface and bottom samples were collected. The depth at which the samples were taken varied with the depth of the river. All sampling stations were in mid-stream, no account being taken of the possible variations of plankton density across the river. The position of each station is indicated in Fig. 1.

For phytoplankton studies, 250 ml. of sample were preserved with 4% formalin and stored in screw-capped jars for later examination. The density of phytoplankton was determined by transferring, with a wide-mouthed pipette, 1 ml. of well-shaken sample into a 1 ml. Naumann counting chamber. Counts were made under a $\frac{1}{2}$ in. objective of fifteen fields selected at random, two counts being made from each sample. When the density of phytoplankton was less than 500 organisms/ml., the samples were concentrated by centrifuging 10 ml. at 2000 r.p.m. for 5 min., withdrawing the upper 9 ml., and counting the phytoplankton in the 1 ml. remaining.

For zooplankton, each 2 l. sample was concentrated in the field by sieving through a nylon net with a mesh size of $20–50 \times 50–80\ \mu$. All the organisms in these samples were counted and average densities per unit volume determined for each level and station. At most stations samples were also collected with a net of the standard Windermere type, by letting the nets float downstream from the moored boat for 10–20 min. These samples were used to furnish additional information on plankton components.

Chemical and physical observations were made at each station. Water temperatures, turbidity and pH were measured in the field, while samples for later determinations of dissolved oxygen concentrations, total dissolved solids and alkalinity, were also collected.

Estimations of plankton densities are subject to technical, biological and statistical errors, and thus the smaller the sample unit the more marked will these errors be. Therefore, in drawing general conclusions, all samples taken at each station have been grouped and averaged. The results that follow express only the approximate representation of the main plankton components at the mid-stream stations indicated during the period of the investigation and do not show total production, since this was not the period of maximum productivity. Within these limits the results, nevertheless, show an unmistakable trend and a reasonable consistency.

PHYSICAL AND CHEMICAL MEASUREMENTS

(*a*) *Turbidity*

(Measured with a Secchi Disk)

It might be expected that turbidity would decrease as the influence of the dam became more pronounced, owing to the slowing down of the current and consequent settling of suspended matter. This was, however, masked by the vast production of plankton in the vicinity of the dam. Although the settling of suspended matter was observed, detritus becoming more abundant in succeeding samples taken upstream, turbidity in fact increased towards the dam.

(*b*) *Total dissolved solids*

(Measured by electrical conductivity)

The higher concentration of dissolved salts in the region of the dam (Fig. 2), may perhaps be interpreted as due to the liberation of solutes from the flooded ground.

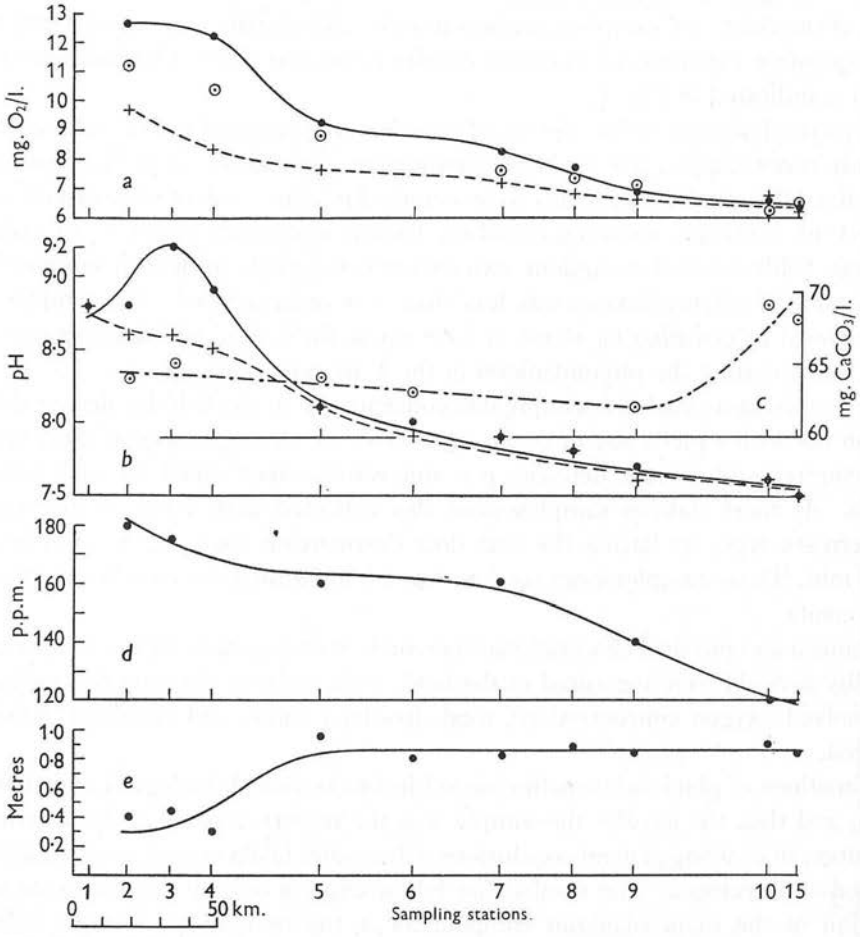

Fig. 2. Physical and chemical measurements. (*a*) Dissolved oxygen: ●—●, surface; ⊙, mid-depth; + – – +, bottom. (*b*) pH: ●—●, surface; + – – +, bottom. (*c*) Alkalinity. (*d*) Total dissolved solids. (*e*) Visibility of the Secchi disk.

(*c*) *Alkalinity and* pH

(The former estimated by titration against standard N/100 HCl; the latter colorimetrically in the field with a B.D.H. Comparator)

Alkalinity, measured as mg. $CaCO_3$/l., shows only a very slight decline between the dam and station 9, and this is followed by an increase beyond. The pH, on the other hand, shows a marked rise which cannot be accounted for by these changes in alkalinity. It seems rather to be correlated with the photosynthetic activity of the phytoplankton removing the dissolved CO_2, this being most marked in the neighbourhood of the dam (see also data for dissolved oxygen concentration). Experiments carried out on the

White Nile a few weeks before the present investigation, when the phytoplankton density was 10,000 organisms per ml. (*Anabaena flos aquae* and *Melosira granulata* dominant), revealed marked diurnal changes in pH, from about 8·0 during the night to a steady value of 9·2, attained an hour after sunrise, thus confirming the present results.

(*d*) *Dissolved oxygen concentration*

(Estimated by Winkler's method)

As with pH, it seems that the dissolved oxygen concentration can be directly correlated with the amount of phytoplankton. The relevant graph shows that not only was the O_2-concentration greatest where the phytoplankton was most abundant, but also that the differences in concentration between the upper and lower layers were greatest in these regions. Although the density of phytoplankton tended to be greater in the surface layers (Table 1), these differences were not large, and consequently it is thought that the differences in oxygen concentration are rather a reflexion of the reduction in light intensity in the lower layers caused by the dense growth of the plankton and the accompanying lessening in photosynthetic activity. This contention is supported by the differences in pH at different depths which have been recorded in these regions, the greatest values being found in the surface layers.

THE COMPOSITION OF THE PLANKTON

(*a*) *The Phytoplankton*

Observations extending over a period of three years show that the phytoplankton of the White Nile between Khartoum and the Gebel Aulyia Dam (15 km. north of station 1—see Fig. 1), is composed principally of diatoms and blue-green algae, and hence resembles that of a typical eutrophic lake. At the time of the present study, blue-green algae were dominant: samples taken on 10 December near Khartoum indicated that this group comprised 83% while diatoms formed 15% and Chlorophyceae 2% of the total population.

The dominant alga was *Anabaena flos aquae*, var. *intermedia*, forma *spiroides* Woronich, with *Lyngbya limnetica* Lemm. approaching it in importance. The principal diatom was *Melosira granulata* (E.) Ralfs, and the var. *angustissima* Müll. Also present in considerable numbers were *Anabaenopsis Cunningtonii* R. Taylor, previously recorded only from Lake Tanganyika, *A. Tanganyikae* (G. S. West) Wolosz. & Miller, *Raphidiopsis curvata* Fritsch, not previously recorded from the Nile, *Oscillatoria geminata* (Menegh.) Gom. and *O. planktonica* Wolosz. Other diatoms were *Melosira Agassizzii* Ostenf., *Synedra acus* Kg., *Nitzschia acicularis* W. Sm. and *N. palea* (Kg.) W.Sm. The Chlorophyceae were mainly represented by *Ankistrodesmus falcatus* (Corda) Ralfs, *Scenedesmus acuminatus* (Lagerh.) Chodat, *Micractinium pusillum* Fresen. and *Dictyosphaerium pulchellum* Wood. All of these algae have also been found upstream of the dam during the present investigation, though their distribution and abundance varies considerably throughout the stretch of river studied (see Table 1 and Fig. 1).

Table 1. *Density of phytoplankton at different depths at different stations*

(Figures give the number of organisms per 0·1 ml. Species and group maxima are shown in heavy type: + indicates present.)

Station ...	1			2			3			4		5			6		7			8			9			10			15		
Sampling depth (m.) ...	0	3	6	0	5	9·5	0	2	4·5	0	1·5	0	5	9·5	0	2·5	0	2	4·5	0	4·5	8·5	0	3·5	7	0	3	5·5	0	3	4·5
Melosira granulata	50	53	**65**	51	39	48	48	53	51	31	51	10	10	10	6	6	2	3	1	3	2	2	2	2	2	1	1	1	1	1	1
M. granulata, var. *angustissima*	20	**36**	10	22	24	24	34	27	22	29	15	4	5	5	3	4	2	2	2	1	1	1	1	1	1	1	2	1	1	2	3
Raphidiopsis curvata	**29**	**29**	12	10	15	7	+	5	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Anabaenopsis Cunningtonii	44	**46**	36	17	17	24	+	5	5	2	10	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
A. Tanganyikae	**20**	12	+	+	10	+	+	+	–	5	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Anaebana flos aquae	236	217	253	220	147	152	**310**	128	108	147	145	–	1	+	+	+	+	–	–	–	+	+	–	–	–	–	–	–	–	–	–
Anabaena spp.	22	12	20	**32**	10	12	15	15	2	2	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Oscillatoria geminata	41	**50**	34	46	41	29	12	5	24	20	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
O. planktonica	**44**	22	22	32	19	32	15	7	7	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lyngbya limnetica	**215**	162	154	138	150	100	46	60	53	49	65	+	1	–	1	1	–	+	–	–	–	–	+	–	+	+	–	+	+	+	+
Totals																															
Chlorophyceae*	+	+	5	+	**12**	5	5	+	3	3	–	1	+	+	2	1	1	1	1	2	2	1	1	1	1	1	1	1	+	+	+
Diatoms*	89	**114**	89	94	80	99	82	79	89	81	84	16	16	16	11	11	6	7	5	6	6	5	6	6	5	4	5	5	4	4	4
Cyanophyceae	**660**	550	530	501	410	360	420	226	203	243	240	1	2	1	1	1	1	1	+	+	+	+	1	+	+	+	+	+	1	+	1

* See p. 105 for list of principal diatoms and Chlorophyceae present.

(*b*) *The Zooplankton*

Of the zooplankton only the Crustacea have been identified specifically; the taxonomy of many tropical Entomostraca is at present unsettled and certain species or varieties here listed will be defined more clearly in the future. The Rotatoria were counted as a group while the Protozoa were not investigated because of technical difficulties. At the time of the investigation and in the region of the river studied, the following species formed the bulk of the Crustacean plankton:

Diaphanosoma excisum Sars, near but not quite identical.
Ceriodaphnia rigaudi Richard, with round and horned individuals present.
C. dubia Richard, not quite identical.
Moina dubia de Guerne & Richard, very variable.
Daphnia lumholtzi Sars.
D. barbata Weltner.
Cyclops (*Thermocyclops*) *neglectus* (Sars)
C. (*Mesocyclops*) *leuckarti aequatorialis* Kiefer, in two sizes.
Diaptomus galebi Barrois.

There is a clear distinction between the above truly planktonic forms and the adventitious species from the shore, bottom and side waters. The following additional forms have been found in the quantitative and net samples:

Arcella, *Difflugia*, *Hydridae* sp. } some of these may be truly planktonic.
Turbellaria, in bottom layers.
Cercariae of Trematodes.
Oligochaeta spp.
Urnatella (Bryozoa) fragments.
Phyllopoda: species of *Cyclestheria*, *Latonopsis*, *Pseudosida*, *Simosa*, *Pseudoalona*, *Euryalona*, *Camptocercus*, *Leydigia*, the *Alona* group, *Chydorus*, *Ilyocryptus*, *Macrothrix*, *Grimaldina*.
Copepoda: *Diaptomus processifer*, sp. of *Microcyclops*, *Paracyclops* and others.
Ephemerid nymphs, Chironomid larvae, Hydracarina.

The occurrence of these non-planktonic forms at certain stations seems to be significant and will be discussed later.

THE GENERAL DISTRIBUTION OF PLANKTON DOWNSTREAM

The densities of the main species and groups of phyto- and zooplankton at each collecting station and depth investigated are set out in Tables 1 and 2 respectively, while the total densities of phyto- and zooplankton, averaged for each station, are plotted in Fig. 3.

It is apparent that within the 352 km. from station 15 to the dam, the plankton as a whole showed a very marked numerical increase. For both plants and animals this was more than 100-fold, the river at station 15 carrying 49×10^3 algae and 0·8 animal per litre, rising to maxima of 6790×10^3 and 123 per litre respectively in the vicinity of the dam. The increase was at first slight, becoming marked at about 250 km. from the dam, but being rapid only in the final 100 km. The increase in phytoplankton continued beyond the dam, the richest sample being obtained at station 1, some 19 km. below, whilst the greatest density of zooplankton was at station 3, 19 km. above. At station 2, 1·2 km. above the dam, samples showed a marked decrease in zooplankton

Table 2. *Density of zooplankton at different depths and different stations*

(Figures give the number of organisms per litre. + Indicates organisms present at estimated density of 0·25/l.)

Station ...	1			2			3			4	5			6		7			8			9			10			15		
Depth (m.) ...	0	3	6	0	5	9·5	0	2	4·5	0*	0	5	9·5	0	2·5	0	2	4·5	0	2	8·5	0	3·5	7	0	3	5·5	0	2	4·5
Diaphanosoma excisum	2	–	3	4	–	–	5	1	4	2	1	1	1	+	1	–	+	+	–	–	–	–	–	–	–	–	–	–	–	–
Ceriodaphnia rigaudii	44	6	30	54	3	8	105	17	37	17	5	2	7	3	1	1	1	1	+	+	–	–	–	–	–	–	–	–	–	–
C. dubia	1	–	–	1	–	1	1	+	1	+	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Moina dubia	–	–	1	1	–	+	1	+	+	1	+	1	+	1	1	+	+	–	1	–	+	–	–	–	–	–	–	–	–	–	–
Daphnia lumholtzi	–	–	–	1	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
D. barbata	–	–	–	–	–	–	–	+	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Thermocyclops neglectus, female	–	–	1	4	1	1	2	–	1	1	+	–	–	1	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
T. neglectus, male	1	–	1	1	–	–	2	–	+	+	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–
Mesocyclops leuckarti aequatorialis, female	–	–	–	1	–	–	1	–	1	+	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
M. leuckarti aequatorialis, male	–	–	–	1	–	+	1	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cyclopidae, juvenile	5	1	4	4	–	1	4	1	3	4	1	1	1	1	1	–	–	–	1	+	–	+	–	–	–	–	–	1	+	–
Cyclopidae, nauplii	30	14	45	16	5	10	58	12	22	12	6	5	8	5	3	1	+	1	1	1	+	+	1	+	1	+	1	–	+	–
Diaptomus galebi, female	–	–	1	2	–	–	1	–	+	–	1	–	–	–	–	1	1	1	–	–	–	–	–	–	–	–	–	–	–	–
D. galebi, male	–	1	–	4	–	–	1	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
D. galebi, juvenile	2	1	4	11	–	–	5	2	2	3	1	+	+	–	1	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
D. galebi, nauplii	9	1	9	2	1	2	7	1	2	3	1	1	1	2	1	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–
Rotatoria	17	10	13	6	5	5	47	12	12	10	7	2	4	12	3	4	5	3	6	–	–	+	–	–	–	–	–	–	–	–
Adventitious forms	–	–	1	–	–	1	–	–	1	–	–	–	–	–	–	+	–	–	–	–	1	–	–	2	–	1	+	+	+	+
Total population	110	32	111	109	16	30	241	46	87	52	23	13	23	25	11	7	7	6	9	1	1	1	1	2	1	1	1	1	1	+
Average population at each station	84			52			125			52	20			18		7			4			1			1			1		

* Samples from 1·5 m. at station 4 were lost.

which may have been due to the increase in current near the dam's sluices; this tends to be confirmed by the reappearance here of adventitious forms. Since two of the samples from this station were lost, too much weight cannot be attached to this observation. Two other sets of samples from station 2, one taken shortly before and the other shortly after the present investigation, showed plankton densities of 73/l. on 8 December and 103/l. on 29 December 1951. All three samples thus show a decrease, compared with the 123 organisms/l. at station 3. In the graph (Fig. 3), all three figures have been plotted and the graph drawn through the average (73·8) of these densities.

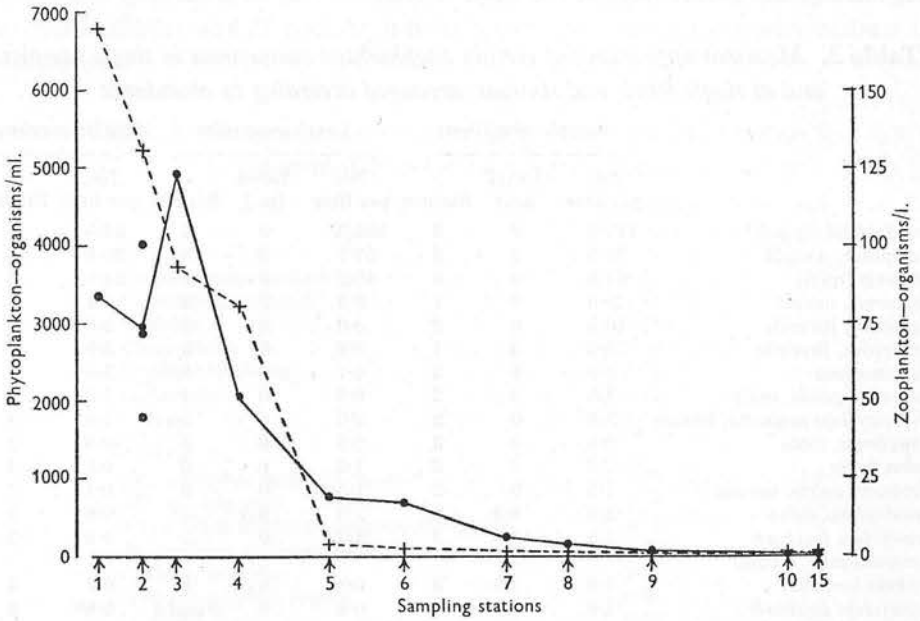

Fig. 3. Average density of phytoplankton (+ – – +) and zooplankton (●—●).

THE DISTRIBUTION OF THE PLANKTON COMPONENTS AND THE LOCAL DIFFERENTIATION OF THE PLANKTON

The results considered above are based on the total density of plankton at each station. The role which each plankton component plays in the downstream and vertical distribution will now be considered.

(*a*) *The Phytoplankton* (Table 1)

Consideration of Table 1 shows that all species reached their maximum development in the three stations (2, 3 and 4) nearest the dam, though many of them continued to multiply for some miles below it. This may be due to the mixing and better aeration of the water as it passes through the sluices. That such mixing does take place seems to be indicated by the vertical distribution of several of the more abundant species. Between stations 15 to 5, where the phytoplankton is scarce and river-like conditions apparently predominate (Fig. 1), the distribution in depth seems to be a random one. Downstream of station 5, many species show a tendency to reach their greatest density at the surface and in the middle depths, and at stations 1 to 4, all total

maxima occurred at these depths. It is clear from Table 1 that the dominant group of algae, the Cyanophyceae, showed a tendency to assemble near the surface in the lake-like stretch (stations 2–5), though diatoms appeared to remain evenly distributed. Station maxima of the commonest species (> 300/ml.) of Cyanophyceae at stations 2–4 also tended to be at the surface, but at station 1, where the 'lake' has reverted to river, two species (*Oscillatoria planktonica* and *Lyngbya limnetica*) had maxima at the surface, two (*Anabaenopsis Cunningtonii* and *Oscillatoria geminata*) in the middle layers, and the dominant *Anabaena flos aquae* at the bottom, suggesting some mixing of the plankton as water passes beyond the dam.

Table 3. *Maximal appearance of certain zooplankton components in single samples and at single levels and stations, arranged according to abundance*

	Sample maximum			Level maximum			Station maximum	
	No. per litre	Level (m.)	Station	No. per litre	Level (m.)	Station	No. per litre	Station
Ceriodaphnia rigaudi	117·0	0	3	104·5	0	3	52·5	3
Cyclopidae, nauplii	70·0	0	3	57·7	0	3	30·6	3
Rotatoria (total)	53·5	0	3	46·2	0	3	23·5	3
Diaptomus, nauplii	9·0	0	1	6·5	0	3	6·1	1
Diaptomus, juvenile	10·5	0	2	5·0	0	3	2·8	3
Cyclopidae, juvenile	5·0	0	1	3·8	0	3	3·8	4
Diaphanosoma	5·0	0	3	4·7	0	3	3·3	3
Diaptomus galebi, male	4·0	0	2	0·8	0	4	1·0	2
Thermocyclops neglectus, female	3·5	0	2	2·0	0	3	1·4	2
T. neglectus, male	2·5	0	3	2·3	0	3	0·8	3
Moina dubia	2·5	0	3	1·3	0	3	0·8	4
Diaptomus galebi, female	1·5	0	2	1·5	0	3	0·4	2
Ceriodaphnia dubia	2·0	9·5	2	1·3	9·5	2	0·9	2
Mesocyclops leuckarti aequatorialis, female	1·5	0	3	1·3	0	3	0·6	3
Daphnia barbata	1·0	4·5	3	0·8	4·5	3	0·3	3
Mesocyclops leuckarti aequatorialis, male	1·0	0	4	0·8	0	3 and 4	0·8*	4
Daphnia lumholtzi	0·5	5·0 4·5	2 3	0·5	4·5	3	0·3	2

* Only one level at this station.

(*b*) *The Zooplankton* (Table 2)

All species of Cladocera were represented by a majority of parthogenetic females; further inquiry into the sexual processes has been left to the future. In the Copepoda, sexes and stages were counted separately; juvenile forms of Cyclopidae counted together; Rotatoria were treated as a whole; similarly non-planktonic (adventitious) forms.

Each species, and each group of animals, shows a gradual increase towards the dam; or upstream, a thinning out which leads to the disappearance of some species from the quantitative samples. In the typical river stations from 9 upstream juvenile *Cyclops* and Rotatoria, besides adventitious forms, were alone sufficiently numerous to appear in the volumes of water examined (12 l. at each station). At such places, net samples clearly afford a more accurate picture of the plankton's composition.

Quantitative data have been assembled in Table 3 to give details of the maximal appearance of certain components arranged to show the maximal occurrence in any one sample (sample maximum), in all samples from one level at each station (level

maximum), and in all samples from all levels at each station (station maximum). This table shows that all the seventeen plankton components have their maximum concentration in the four stations nearest the dam, showing, as in the case of the phytoplankton, that the greatest development takes place in the last 50 km. above the dam, though data from station 1 indicate that the increase of some species may persist for some miles below it. Sample and level maxima show considerable differences, which suggest that even in a limited space, the horizontal distribution is uneven and that a representative picture of the fauna cannot be gained from single 2 l. samples. Sample and level maxima occur mainly at the surface, except for *Ceriodaphnia dubia*, *Daphnia lumholtzi*, and *D. barbata*, but for which the data are too scanty to draw any conclusions.

Table 4. *Percentage occurrence of zooplankton species at station 3, quantitative and net samples compared*

	Quantitative samples	Net samples
CLADOCERA		
Diaphanosoma excisum	4·9	3·7
Ceriodaphnia rigaudi	79·4	79·7
C. dubia	1·08	1·0
Moina dubia	0·88	1·0
Daphnia lumholtzi	0·25	—
D. barbata	0·51	0·3
Total	87·0	85·7
COPEPODA		
Thermocyclops neglectus, female	1·38	1·7
T. neglectus, male	1·26	0·3
Mesocyclops leuckarti aequatorialis, female	0·76	0·3
M. leuckarti aequatorialis, male	0·37	—
Cyclops, juvenile	3·5	1·0
Diaptomus galebi, female	0·5	1·7
D. galebi, male	0·63	3·3
D. galebi, juvenile	4·78	6·0
Total	12·75	14·3

Data on the vertical distribution of the zooplankton can also be gleaned from the total population numbers in Table 2. Although the material is scanty, a few conclusions seem to be justified. Surface samples are richest at stations 2, 3, 6 and 8, while bottom and surface samples were equally rich at 1 and 5. Middle layers were least populated in 1, 2, 3 and 5, whilst the differences in vertical distribution are insignificant in the true river stations, i.e. 7, 9, 10 and 15. It would seem that under normal river conditions, outside the influence of the dam, there is little stratification. The more lake-like the conditions become, however, the more the ever-increasing plankton population is differentiated into strata.

There is an appreciable difference in the value of quantitative data for the phytoplankton and for the zooplankton, for the former is always present in measurable amount while the latter diminishes to such a degree upstream that it cannot be estimated even in a series of 12 l. samples. Net samples have therefore been used to provide additional information about the occurrence of the zooplankton components. In each net sample 3×100 specimens were counted, excluding nauplii and Rotatoria,

which are only partly caught. The percentage occurrence of the fourteen pure plankton components in the net plankton was compared with their occurrence in the quantitative samples, calculated anew with the omission of nauplii and Rotatoria. Table 4 shows for station 3 the similarity in percentage occurrence in quantitative as compared with net samples.

Similar calculations and comparisons, made for all stations for which sufficient material was available, afforded results comparable to those given above. In Table 5 only the total percentage occurrence of Cladocera, Copepoda and adventitious forms in quantitative and net samples is given for each station. There are considerable differences between quantitative and net samples in the case of the adventitious forms. This is because net hauls were taken from the surface, whilst adventitious forms are usually more plentiful in the deeper layers. Nevertheless, it seems possible to trace a trend in the representation of the zooplankton components. The net samples also amplify the picture of the zooplankton in the upper stretches of the river. They show

Table 5. *Total percentage occurrences of zooplankton by groups*

*=no net sample taken; + =less than 0·5% occurrence.

	Cladocera		Copepoda		Adventitious	
Station	Quant.	Net	Quant.	Net	Quant.	Net
1	81	*	18	*	1	*
2	72	74	26	26	2	+
3	87	86	13	14	+	—
4	68	*	32	*	—	*
5	80	87	20	13	—	+
6	60	75	40	25	—	—
7	60	67	35	31	5	1
8	36	68	43	30	21	2
9		26		61		14
10	5	29	32	47	64	25
15		14		64		23

Because of the small numbers of organisms present the quantitative samples for stations 9, 10 and 15 have been grouped and averaged.

that the disappearance of certain components in the quantitative samples from upstream is only due to their diminution, since only *Ceriodaphnia dubia* and the two *Daphnia* species disappear from the net samples of the true river stations (9, 10 and 15), whereas all the others were recorded, though in very small numbers.

From Tables 1 and 5 it is now possible to trace the distribution of the main components of the plankton, and reconstruct a picture of the gradual changes in its composition. In the region farthest from the dam the plankton consists of a sparse community of plants and animals, including truly planktonic, along with bottom- and shore-inhabiting species. These are carried downstream in the turbulent water, rich in detritus and dark in colour. Of the plants, diatoms (principally *Melosira granulata*) constitute 75–90% of the population, with Chlorophyceae (mainly *Ankistrodesmus falcatus* and *Scenedesmus* spp.) next in importance (8–21%), a sparse population of Cyanophyceae (about 5%) and a few dislodged epiphytic algae. Associated with these is a zooplankton of Copepoda (32–63%) and Cladocera (5–29%), along with

a considerable proportion of adventitious forms, comprising 14–24% and in places rising to 60% of the whole population.

This mixed community, in part truly planktonic, is carried downstream until, apparently at about 240 km. from the dam, it becomes noticeably affected by changes in hydrological conditions. Detritus and adventitious forms settle out and the water becomes conspicuously cleaner. As lake-like conditions develop, the true planktonts find their particular requirements and begin to multiply rapidly. Not only does the density of the plankton increase, but its composition changes. For the zooplankton the crucial turning point is between stations 8 and 9. Up to there Copepoda are dominant, but between station 7 and the dam Cladocera (60–87%) dominate the Crustacean plankton, while Copepods show a relative decrease (12–40%). Adventitious forms disappear altogether in this region, though they reappear near the sluices of the dam, presumably being swept into the plankton with the increased flow of water. The turning point for the phytoplankton is much nearer the dam, the marked change in the relative importance of its constituents accompanying the vast increase in productivity between stations 5 and 4. Diatoms, which are dominant in the upper reaches, decrease from 93 to 31%, while Cyanophyceae become the dominant group, increasing from 5 to 86% of the total population. Nevertheless, all three groups increase numerically as the dam is approached and continue to increase beyond it.

Previous workers have noted that the quality and quantity of the zooplankton may be closely related to the nature of the phytoplankton. Lèfevre (1948), for example, describes changes from a rich to a poor zooplankton which were associated with a change from a chlorophycean to a cyanophycean phytoplankton. The vast development of Cyanophyceae in the plankton near the dam may thus have been an additional factor causing the decline in zooplankton at station 2. Although the biological effects of impounding water by dams have been previously observed, notably by American authors, it seems premature at this stage to compare the present results from one short period of observations, with those gained elsewhere. As far as can be ascertained, however, no quantitative data from any African river, or indeed from any large tropical river, have been published. Consequently, the present paper is regarded merely as fact finding and only a contribution to the extensive study of Nile biology which is in progress.

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SUMMARY

1. The biological effects of impounding water by a dam have been investigated on the White Nile, by taking a series of plankton samples from the Gebel Aulyia Dam upstream for 352 km.

2. From the sampling station farthest from the dam to the dam itself, the plankton showed a numerical increase of more than 100-fold, the phytoplankton rising from 49 to 6790×10^3 and the zooplankton from 0·8 to 123 organisms per litre. This increase

has been related to the changes from river to lake-like conditions. The maximum density of both phyto- and zooplankton was attained in the last 50 km. above the dam.

3. Changes in the composition of the plankton were also observed. In the upper regions it was mixed with non-planktonic forms, whilst of the truly plankton forms, diatoms and copepods predominated. With increasingly lake-like conditions the adventitious forms disappeared and Cyanophyceae and Cladocera gained dominance.

4. Some physical and chemical factors were investigated. Although there was a loss of suspended detritus, turbidity increased owing to the vast development of phytoplankton near the dam. The dissolved oxygen concentration and the pH also showed marked increases, which have also been correlated with the rich phytoplankton near the dam.

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Seasonal plankton development in the White and Blue Nile near Khartoum

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With 2 figures and 2 tables in the text

The Nile system consists of two main rivers, the White Nile which flows 2600 km from the Central African Lake Plateau and the Blue Nile which comes 1600 km from the Abyssinian Plateau to their junction in the Sudan plains at Khartoum. From here the joint Nile flows a further 3000 km through 5 cataracts and the Aswan dam towards its Mediterranean Delta. The White Nile, called by different names in its upper course, is the second or third longest river in the world, traversing 35 degrees of latitude from south to north and passing through a series of climatically and geographically different regions.

The natural flow of the river system has been altered for irrigation purposes. On the White Nile the Gebel Aulya dam, built in 1936 44 km south of Khartoum, stores $3^1/_2$ milliards cubic meters of water, forming a large basin of slowly flowing water, whose influence is felt over 400 km upstream. Stored from July to the end of January it is gradually released from February onwards until the basin is emptied to normal river level in May. Besides this artificial storage the natural river discharge of the White Nile does not show any flood phenomenon comparable to that of the Blue Nile. This latter river carries the historically famous silt-bearing flood which comes down after the rains from the Abyssinian Plateau and arrives at the Sennar dam, erected in 1925 360 km southeast of Khartoum, during the second half of June. The peak of the flood in late August or early September has a discharge 40 times greater than the minimal flow in May. The Sennar dam begins to store its 800 millions cubic meters reserve of water in November, when the flood subsides and allows normal river flow, which gradually decreases to its lowest level in May.

These are the main outlines, relevant to our present investigation, of the intricate hydrology of this river system, which has been studied more intensively than that of any other large river (Hurst 1952).

Methods, Material

The biology of the river system in its upper and middle courses has received little direct attention apart from short notes by Ekman, Daday, Gurney and Chappuis. A few years ago regular observations were started on the plankton, this being the most conspicuous hydrobiological feature. In the long term programme covering the exploration within the Sudan, of the 4000 km of main river courses of

Table 1. Densities of zooplankton in the White and Blue Nile at Khartoum.

Each figure represents 1 cubic meter of water,
calculated as mean of 6 samples = 12 liters, from 3 levels.

Date		White Nile			Blue Nile			
Month	Day	Crustacea	Rotatoria	Non-planktonic	Day	Crustacea	Rotatoria	Non-planktonic
1951								
VII	16	4 000	?°	2 000				
VIII	10	—	?	250				
IX	11	48 280	?	?				
	26	57 270	?	?				
X	30	27 750	?	?				
XI	7	22 200	4 400	?	19	1 300	?	?
	17	72 800	6 500	—	23	660	?	?
	24	66 000	3 900	1 100				
XII	4	78 500	2 300	1 000	8	1 370	?	120
	11	58 800	6 080	500	30	8 700	4 600	?
1952								
I	1	58 000	20 000	83	8	16 000	18 100	400
	14	92 700	18 400	500	24	19 000	43 300	700
	29	42 000	18 600	500	28	31 000	36 200	1 160
II	5	57 700	13 800	500	7	42 000	112 500	4 750
	21	50 750	28 000	250	29	13 500	54 100	1 600
III	13	41 650	12 400	650	27	4 300	23 000	580
IV	24	22 500	9 100	300	30	5 500	18 500	—
V	24	1 375	—	125	15	10 500	3 700	250
					31	108 500	54 600	250
VI	8	1 750	375	750	15	76 600	170 000	370
					26	4 250	250	1 000
VII	9	3 625	4 500	625				
VIII	12	17 700	5 100	500				
	24	35 700	2 400	250				
IX	16	108 100	21 500	400				
X	9	98 500	19 100	750				
XI	7	46 400	13 660	330	1	160	—	160
	21	59 000	18 100	330	15	2 170	4 000	—
XII	5	52 400	12 300	2 800	1	16 700	55 300	—
	17	78 100	12 800	3 200				
1953								
I	9	42 500	7 500	1 300	1	12 300	57 000	270
	30	27 000	10 800	600	19	11 000	44 400	580
II	20	32 700	10 000	700	7	5 000	202 900	1 500
					28	6 450	37 000	80
III	26	14 500	3 600	1 400				
IV	13	37 000	8 600	500	2	2 000	19 000	250
					23	6 600	9 800	—
V	20	2 420	3 200	580	25	31 200	49 600	500

° Positions marked with ? have not been determined exactly.

various accessibility so far the Gebel Aulyia basin has been studied (Brook and Rzóska 1954) and a few observations have been made on the Upper White Nile.

Our present notes relate to the two Niles in their final individual stretches shortly before their junction near Khartoum, and describe the annual fluctuations of plankton in each. Quantitative samples were taken from summer 1951 until May 1953 with a Friedinger (Luzern) sampler of 2 liters capacity from surface, middle and bottom levels of midstream, and density figures have been calculated as the means of the 3 levels. Both phytoplankton and zooplankton are treated in general terms; the account of the biology of the individual species will be given at some later date.

Periodicity of zooplankton

The results are given in Table 1 and Fig. 1, from which the following conclusions emerge:

Both rivers show big short period fluctuations in densities of plankton.

The fluctuations are twofold: an annual regular rise in autumn and a decline in spring not completely coinciding in both rivers, and irregular, sometimes sharp fluctuations following successively but not altering the main course of development.

The White Nile at Khartoum shows a preponderance of Crustacea over Rotatoria, the Blue Nile the opposite.

Successive years show differences in densities attained.

The density of zooplankton in the White Nile reaches its lowest level in late May, June and July, when it is mixed with a large percentage of adventitious non-planktonic forms. August brings an increase which rises rapidly to high densities in September to December, and these begin to decline in January and rapidly decrease towards May.

In the Blue Nile there is no plankton discernible in the silt-laden waters of July to October; it begins to appear in November, rising steeply in density to a peak in February, followed by a drop towards March and April. A second rise, almost an "outburst", followed in 1952 in May and early June, and May samples of 1953 show the same tendency. There is an abrupt decrease in late June.

Periodicity of phytoplankton

(Table 2 and fig. 2)

When fully developed, a pure phytoplankton formation appears in both rivers and is composed principally of blue green algae and diatoms, while the less numerous Chlorophyceae are represented by various members of the Chlorococcales.

As with the zooplankton, truly river-like conditions are inimical to the development of this community and it is only when the rates of flow slacken, either through natural causes or under the influence of the dams, that the phytoplankton becomes abundant. In general, after high water and as current speeds diminish,

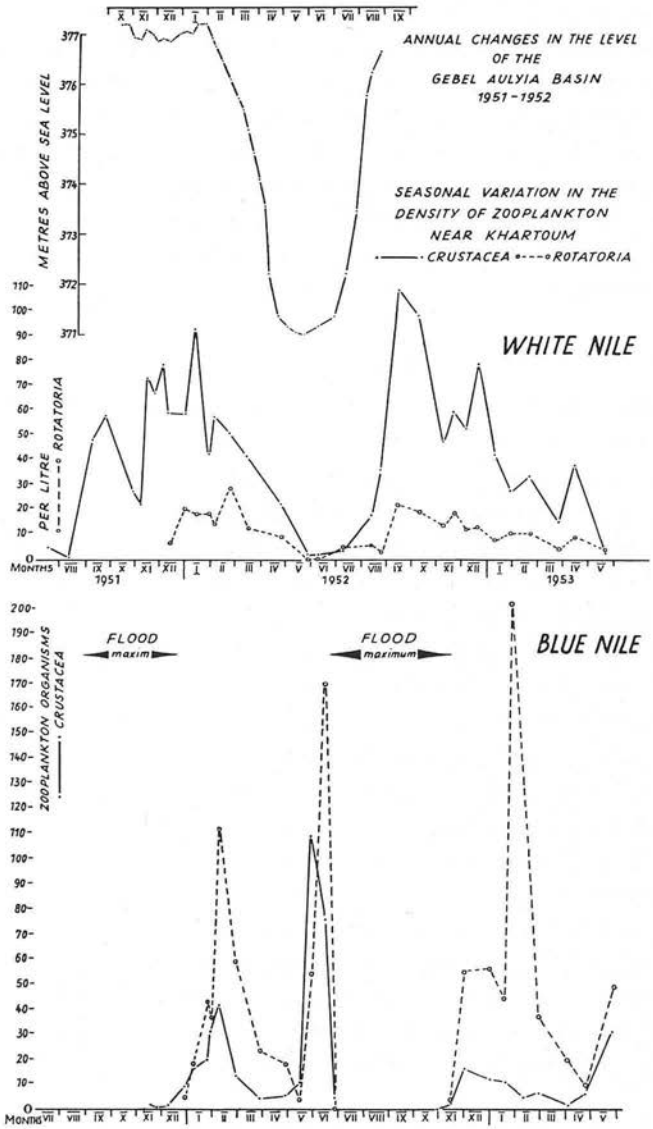

Fig. 1

diatoms are the first group to appear in numbers, the principal species being *Melosira granulata* (E.) RALFS, and its var. *angustissima* MULL. Later, when the flow is further reduced, blue green algae multiply rapidly and soon assume a position of dominance which tends to be maintained until the current speed increases again and the entire plankton is washed out. In both rivers, the dominant blue green alga, which at times produces water blooms, is *Anabaena flos aquae* var. *intermedia* forma *spiroides* WORONICH, though at times *Raphidiopsis curvata*

Table 2. Densities of phytoplankton in the White and Blue Nile at Khartoum. Densities are recorded per ml., and are the average of samples from 3 depths.

Date		White Nile					Blue Nile			
Month	Day 1951	Total	*Melosira*	*Anabaena*	*Lyngbya*	Day	Total	*Melosira*	*Anabaena*	*Lyngbya*
VIII	10	49	47	—	—					
IX	26	310	305	—	—					
X	30	7 410	2 755	205	1 920					
XI	2	7 050	3 940	+	1 780	19	48	10	—	—
	7	8 100	3 100	104	2 200	23	55	7	—	—
	17	10 300	1 350	1 065	2 200					
	24	11 150	1 260	2 683	3 083					
XII	4	10 110	1 290	2 640	3 270	8	73	11	—	—
	11	8 250	710	2 333	2 600	30	663	210	—	—
	1952									
I	1	3 170	630	1 563	470	8	497	360	+	—
	14	2 550	410	1 743	15	24	1 943	675	1 190	—
	29	1 300	313	833	—	28	5 130	556	4 350	—
II	5	2 170	265	1 880	—	7	3 725	170	2 600	—
	21	2 340	433	1 875	—	29	9 250	480	6 800	+
III	5	1 900	720	390	—	27	8 175	805	2 400	+
IV	2	1 620	1 180	310	—	3	2 200	750	1 250	+
V										
VI										
VII										
VIII	24	60	33	—	27					
IX	16	280	140	60	40					
X	9	3 933	1 237	293	1 200					
	31	10 360	2 060	620	7 130					
XI	7	11 043	1 263	273	8 987	15	113	20	13	13
	21	27 840	793	9 800	16 593	29	847	343	50	43
XII	5	24 940	767	14 527	12 273					
	17	12 007	467	9 227	2 500					
	1953									
I	9	3 600	3 373	167	60	1	3 467	760	2 500	20
	30	1 767	1 500	153	20	19	5 133	1 033	3 753	20
II	20	927	827	27	7	7	8 260	4 870	7 583	—
						28	4 047	273	2 560	—
III	26	3 670	553	—	13					
IV	13	1 900	1 647	47	27	2	527	133	40	6
						23	273	93	—	106
V	4	220	30	—	170	14	10 340	2 613	533	5 260
	20	280	140	—	50	25	13 893	13 080	173	126

+ = indicates traces present.

Fritsch and *Lyngbya limnetica* Lemm. may also be abundant. Details of these seasonal changes are given in the accompanying graph and table.

The analysis of samples from different depths suggests that the vertical stratification of the phytoplankton which was observed in the Gebel Aulyia basin (Brook and Rzóska 1954) disappears down-stream.

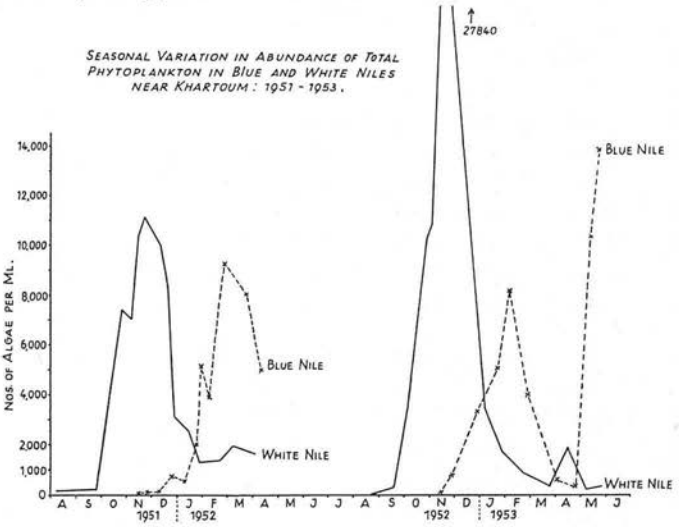

Fig. 2

Spatial and temporal factors of plankton development at Khartoum

In a river the plankton at a particular point at any given moment has not developed there. The local state of its continuously moving "film" must be explained by considerations of time and space. The White Nile, which is more easily accessible, has been investigated in this respect, when in December 1951 a longitudinal plankton section was carried out from Khartoum upstream through the Gebel Aulyia basin to Gebelein (396 km). The results, which have been published elsewhere (Brook and Rzóska 1954), have proved that the White Nile coming from the swamps of the southern Sudan carries a rudimentary, impure plankton and a rich detritus suspension. On entering the large lake-like storage basin of the Gebel Aulyia dam, the current slackens and detritus and adventitious, non-planktonic forms settle out. A pure plankton formation develops, increasing in density towards the dam, with Cladocera gaining dominance in the last 100 km over the Copepods, and Cyanophyceae over the Diatoms and Clorophyceae. This pure lake-like plankton flows through the dam sluices and passes the observation point at Khartoum, again under river conditions. The rich plankton encountered at Khartoum has evidently developed in the basin. The level of the basin decreases rapidly in early February, when the dam is opened to release water for irrigation purposes in Egypt, until the basin is emptied to normal river level in May and June. In July

the dam is closed again, filling to capacity in October. In our graph it is evident then the annual plankton fluctuation at Khartoum follows closely the regular regime of the basin level and is a reflection of the annual plankton cycle in the basin itself (acc. to unpublished material collected by Amin El Tayib). Storage creates favourable conditions while the return to a free flow of the river has unfavourable effects on plankton production. A certain amount of impounding, clearly distinct from a rise in level caused by flood, occurs in the White Nile at Khartoum when the Blue Nile flood in July and August, impedes the flow of the former, thus slowing down the current, raising the level and assisting plankton development. Transparency varies between 20 and 40 cm during the year, the water colour is mostly milky, changing to green shades in October and November.

The Blue Nile shows radical changes in level, water colour and transparency owing to the flood which reaches the Sudan plains in June, following the rains in the Abyssinian Plateau. At Khartoum the clean, bluegreen, low and slow flowing waters of May and early June, with a transparency (Secchi) of almost one meter and a pure plankton formation, suddenly give way to swift, swollen, brown flood conditions at the end of June or beginning of July, with no discernible plankton and transparency at nil. In November with the silt clearing slowly transparency is at 20 cm, and plankton development sets in. The Sennar dam is closed by then and the level of its basin is being raised to full capacity and probably acts as breeding ground. This river stretch, however, has not been investigated and we cannot explain adequately the plankton decrease in March and April from its peak in February, though it might be connected with the free flow of the river at that time. The sudden increases of that pure but impoverished plankton by the end of May and early June might be due to spates, caused by rains in the southern reaches or by the advance of the flood, both of which may push or wash the plankton-bearing-waters downstream. But this is only a hypothesis and has to be substantiated by an investigation of the 620 km stretch from Roseires to Khartoum. The different composition of the plankton with its preponderance of Rotatoria in the Blue Nile may be attributed to its more river-like conditions having a 360 km flow from the Sennar basin as compared with 44 km from the Gebel Aulyia basin before reaching our two observation points at Khartoum.

General remarks

Although their hydrological regime and consequently their biological phenomena differ, both rivers show that a free flow and flood conditions coincide with a decrease of plankton, whilst storage and lowered river levels on the whole favour the increase or at least the persistence of a pure plankton formation. The few observations available from previous workers seem to indicate that before the dams were built "plankton" was scanty and admixed with detritus and adventitious forms. The present conditions seem to a large extent to have been created by human interference.

It would not be profitable at the present stage of our knowledge to comment on the productivity of the Nile waters since no material for comparison from other big tropical rivers seems to be available. We regard the above notes merely as a presentation of facts and as a contribution to a future more complete account in which gradually conditions in all stretches of this vast river system will be explored and correlated with hydrophysical and chemical factors. A hydrobiological research unit with improved river and road transport facilities was created in 1953 and should increase our working potential.

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Summary

Little is known about the biology of the Nile system, of which over 4000 km lie within the Sudan. As part of a long term programme of investigation, now in progress, the plankton of the two main rivers, the White and Blue Nile was examined from 1951 to 1953 at Khartoum shortly before their junction. The regular annual fluctuations of plankton density in both rivers do not coincide completely, but show dependance upon their specific hydrological regimes, which are briefly summarised. The dams erected on both rivers upstream of Khartoum store up water and create favourable conditions for the development of a pure plankton formation. Free flow and flood conditions coincide with a decrease of plankton while storage and low river levels on the whole favour an increase, or at least the persistance of pure plankton.

Discussion

Vaas: The authors' attention is drawn to the similarities and differences between their work and that of Bluche in the Indo-China river system of Grand Lac.

Berg: Do you think that the entomostraca are able to reproduce and to create a new generation, which has time enough to grow up in the running water itself, not in the dam?

Rzóska: Plankton has time and space to develop in such a long river as the Nile. Great densities are, however, reached only when the water has time to "age" more as in storage dams.

Fogg: Does nitrogen fixation of blue green algae in the Nile add to fertility of irrigated areas in the Sudan and Egypt?

Brook: Although there is no definite evidence available, it seems probable that the very abundant growths of blue greens do increase fertility.

A NOTE ON THE ECOLOGY OF THE TERRESTRIAL ALGA, *FRITSCHIELLA TUBEROSA*, IN THE SUDAN

By A. J. BROOK

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A NOTE ON THE ECOLOGY OF THE TERRESTRIAL ALGA, *FRITSCHIELLA TUBEROSA*, IN THE SUDAN

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(*Received* 2 *April* 1955)

(With 1 figure in the text)

It has already been recorded (Brook, 1952) that the terrestrial Chaetophoraceous alga, *Fritschiella tuberosa* Iyengar, makes an annual appearance, between August and October, in the drying silt on the banks of the Blue Nile as the river recedes after the summer floods. The alga grows here in such profusion that it gives a distinctly green tinge to the otherwise bare silt.

The Khartoum plants, though in general agreeing well with the descriptions given by Iyengar (1932) and Singh (1941), nevertheless exhibit certain features not mentioned by either of these investigators. The African plants are similar in showing a clear differentiation into rhizoidal system, tuberous prostrate system and primary projecting system. The secondary projecting system, however, with its elongated cells does not appear to develop under natural conditions in Khartoum. Singh gives details of the soil conditions under which he found *Fritschiella* growing in India and these indicate that the alga can flourish in soils with a moisture content as low as 1.95 per cent. In Khartoum, the alga has never been found to survive in soils with less than 20 per cent moisture content. The temperature, both of the atmosphere and of the soil in the latter place are, however, both extremely high. The average mid-day temperature is 38.7° C. and at certain times, even in soils with a 20 per cent moisture content, and in which the alga has been found to be alive, temperatures of 40° C. have been recorded. Soils with an approximately 2 per cent moisture content have been found to attain temperatures of more than 50° C. in Khartoum and, since no living algae have been found under these conditions, though there was an abundance of dried up, and apparently dead remains of *Fritschiella*, it would seem that it is temperature which is the factor determining the alga's survival in Khartoum rather than soil moisture content.

Related to these observations is the fact that the average relative humidity of the atmosphere is low, being 30 per cent at 2 p.m., during the period when *Fritschiella* is abundant. The approximate mean daily evaporation from an open water surface during the period is 5.8 mm. Khartoum, in fact, lies on the edge of the trade wind desert region, an area which has the highest evaporation rates of any region in the world (Kendrew, 1949). It has already been stated that the more delicate, elongated cells of the secondary projecting system do not develop on the Khartoum plants and it is suggested that this is because of these high evaporation rates. This contention would seem to be confirmed by the fact that considerable elongation of the terminal cells took place when the alga was grown in the laboratory in Petri dishes. Under these conditions there was a considerable reduction in temperature and an increase in humidity, with a consequent

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reduction in the evaporating power of the atmosphere surrounding the alga. In addition to the increase in length, there was also a considerable narrowing of these cells so that they assumed a hair-like condition (Fig. 1), having scanty contents and extremities only 2μ in breadth. Their length, 60 to 100μ, was of the same order as the cells of the second ary projecting systems as described by both Singh and Iyengar. It is of interest to note

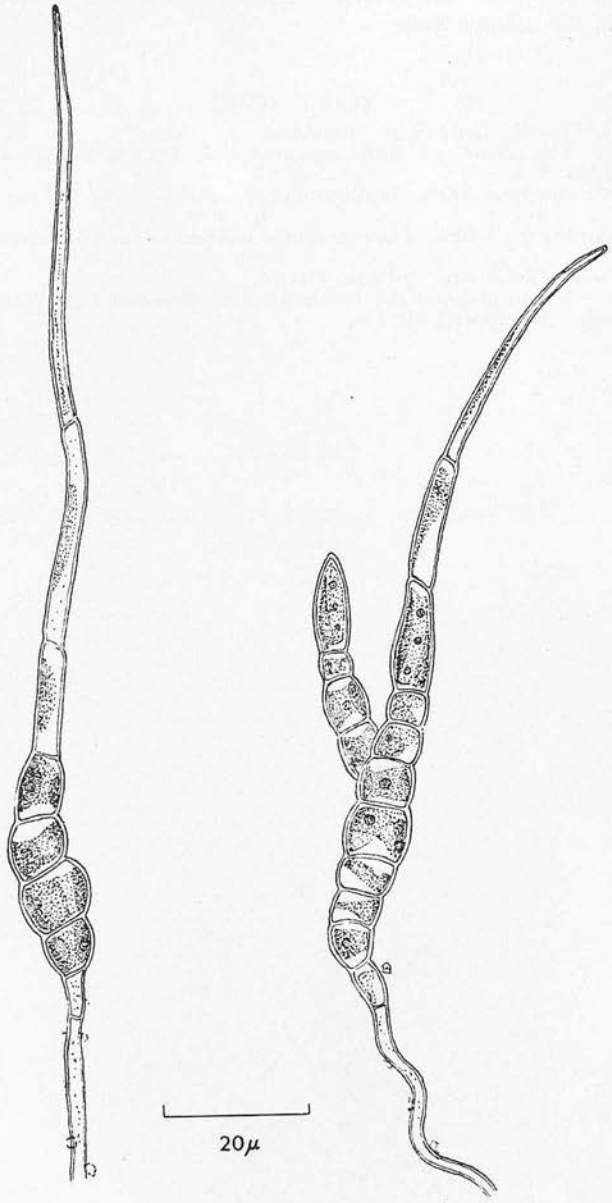

Fig. 1. Specimens of *Fritschiella* grown in Petri dishes in the laboratory. The plant on the left, in particular, shows marked resemblance to *Iwanoffia terrestris*.

that under these conditions the erect system developed without the formation of the typically tuberous prostrate system in which condition the plants then revealed a most striking similarity to the related terrestrial alga, *Iwanoffia terrestris* (Iwanoff, 1900).

Bower (1935), and others, have attached considerable significance to *Fritschiella* in retracing the origin of the land flora and consideration of the exacting environmental conditions under which the alga grows in Khartoum would seem to substantiate the claim that this alga may well have been one of the first successful colonizers in the landward migration of the aquatic flora.

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A bibliography of African freshwater Algae

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■

INTRODUCTION

Within the past decade increasing attention has been devoted to the study of the fresh waters of Africa, as a result especially of the establishment of new fisheries research laboratories in many territories, the increased interest taken in fish-farming projects, and the foundation of new Universities or University Colleges. The situation of some of these latter institutions, as for example the University College of Khartoum and Makerere College, Kampala, near the confluence of the Blue and White Niles, and the East African Lakes respectively, afford excellent opportunities for limnological research. The Gouvernement Général du Congo Belge is also promoting hydrological work on a large scale, both from the purely scientific point of view and on account of its applications to the exploitation of fisheries. As well as the work being done under the auspices of the Institut pour la Recherche Scientifique en Afrique Centrale (I.R.S.A.C.), a number of important hydrological missions have been organised by the Institut Royal des Sciences Naturelles de Belgique, especially those to Lake Tanganyika (1946-7) and to Lakes Kivu, Edward, and Albert (1953-4).

Knowledge of the relevant literature provides the basis for most research, and in the special conditions which exist in many part of Africa, where library facilities are still severely limited, workers new to a particular field may be greatly handicapped. This applies especially in biological studies, where systematics inevitably play

an important part. It is hoped that the following bibliography will help to alleviate this handicap for students of African freshwater Algae, for, with the cheap and rapid methods of photocopying now available, to know what has already been published is the principal step towards possessing the literature.

A bibliography, however, has an additional function, for it reviews, admittedly uncritically, the work already attempted in a particular field, and accordingly reveals some of the gaps in our knowledge. Some of those in the field of African freshwater Algae are emphasised in the present bibliography by the regional index which is appended, and by the map (fig. 1). These indicate clearly that there are still many regions of the continent about whose freshwater Algae we know little or nothing. For example, in contrast to the considerable literature on the Algae of North Africa, East Africa, and South Africa there are surprisingly few contributions both from the whole of West Africa and from the North East. Furthermore, while most of the large African lakes have been studied, there are very few papers dealing with the great rivers which are such important limnological features of the continent. Of these, the Nile has been investigated to some extent, the Congo and Zambesi a little, but the Niger scarcely at all, a glaring omission. An important and fundamental gap of a different sort is our very poor knowledge of the physics and chemistry of the inland waters of Africa, which are often far from fresh, a fact which explains many of the differences between their algal flora and that of European fresh waters.

This list is a combination of two. One was begun by BROOK whilst he was at Khartoum and continued, after his return to Great Britain, largely by Miss SIMS, with the advice and assistance of Ross, in the British Museum (Natural History). The other was prepared in Brussels by H. KUFFERATH, principally in connection with his researches on the African Algae collected by the Mission Hydrobiologique du Lac Tanganyika (1946-1947) (KUFFERATH in preparation). We came to know of each other's work at about the stage when we each thought we were almost ready for publication, and decided to combine at the suggestion of Dr BOURRELLY. When we did so, each list was found to contain a considerable number of papers not in the other.

We have endeavoured to list all papers published up to the end of 1955 on the recent Algae of the inland waters of Africa, whether fresh or saline. We have not included those dealing with fossils, of which there are a number, especially on the beds of freshwater diatoms which are widespread in the continent. The geological

exploration of Africa is so recent that the study of these is very little advanced, but a list of the publications which have so far appeared will be published later. The original publication has been consulted in every case, Miss SIMS having done the bulk of this work. We have used our best endeavours to see that this bibliography is free from error, but realise that this is more than we are

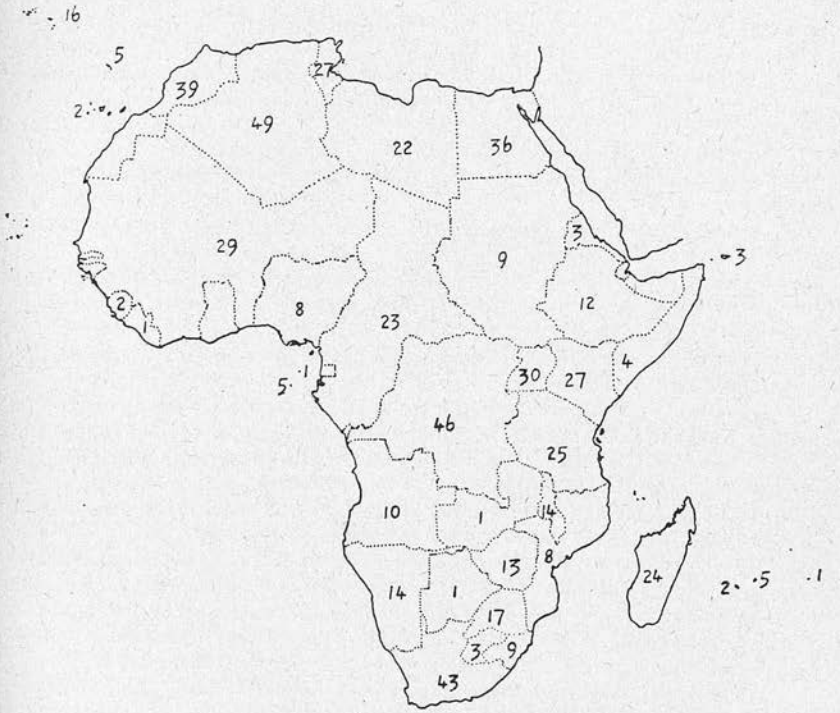

Fig. 1. Geographical Distribution of References to Freshwater Algae in Africa. (Figures indicate the number of papers referring to each territory or region).

likely to have achieved. We should be grateful to have our attention drawn to any omissions or errors so that, if necessary, a supplement can be issued. The titles of journals have been abbreviated as in the « World List of Scientific Periodicals » 3rd. edition, London, 1952.

There are many people to whom our thanks are due, but we wish especially to acknowledge the generous assistance given us by Mr. M. JOLIFFE, Librarian of the University College of Khartoum, Dr. J. W. G. LUND of the Freshwater Biological Association,

all the staff of the General Library of the British Museum (Natural History), and especially Miss P. I. Edwards, Librarian of the Museum's Botany Department. We are also very grateful to Dr. Bourrelly for arranging the publication of this bibliography in the Revue Algologique.

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West G. S. 1909a.
Zahlbruckner 1904.

ERITREA

De Toni G. B. 1891; 1904.
Grunow 1886.

ETHIOPIA

Braun 1867.
Brunelli & Cannicci 1938; 1940.
De Toni G. B. 1892.
Forti 1910.
Grunow 1886.
Lagerheim 1893.
Marchesoni 1939.

Mattirolo 1932.
Nordstedt 1889.
Schmidle 1898.
Zanon 1941b.

FRENCH EQUATORIAL AFRICA

General

Amossé 1941.
Castracane 1887.
Cramer 1868.
Frémy 1924b; 1936.
Leuduger-Fortmorel 1898.

Cameroons

Gutwinski & Chmielewski 1906.
Krieger 1930.
Lefèvre 1932.
Nordstedt 1897.
Pascalet 1934.
Schmidle 1899a; 1901b.

Chad

Dangeard 1940.
Petit & Courtet 1906.

Congo

Frémy 1930b.
Gauthier-Lièvre L. 1954.
Hariot 1896.

Gabon

Dangeard 1947.
Frémy 1930b.
Hariot 1896.

Ubangi-Shari

Frémy 1923b; 1924a.

FRENCH WEST AFRICA

General

Amossé 1941.
Chevalier 1920.
Ehrenberg 1848b.
Gauthier-Lièvre L. 1949.
Leuduger-Fortmorel 1898.
Nordstedt 1880.

Dahomey

Corillon 1952.
Hustedt 1910.
Zanon 1941a.

French Guinea

Frémy 1945.
Gauthier-Lièvre L. 1954.
Hieronymus 1895.
Schnell 1952.
Zanon 1941a.

Ivory Coast

Gauthier-Lièvre L. 1954.
Mangenot 1948.
Zanon 1941a.

Sahara (Mauritania, French Sudan, Niger Colony).

Gauthier-Lièvre L. 1951.
Hariot 1913b.
Monod 1939; 1952; 1954.

Senegal

Grunow 1870; 1880.
Guermeur 1954.
Monod 1952.
Trochain 1940.

Togoland

Zanon 1941a.

Upper Volta

Gauthier-Lièvre L. 1954.

ITALIAN SOMALILAND

Chiovenda 1916.
Frenguelli 1929.
Mattirolo 1929; 1932.

KENYA

Bachmann 1936; 1939.
Beadle 1932a,b.
Borge 1928.
Borgert 1907.
Cunnington 1920.
Daday 1907; 1910a.
Ehrenberg 1851.
Hustedt 1922.
Migula 1904.
Naumann 1925.
Ostenfeld 1908; 1909.
Rich 1931; 1932a; 1933.
Ross 1955.
Schröder 1912.
Virieux 1913.
West G. S. 1907.
West W. & G. S. 1896.
Woloszynska 1914.
Worthington 1930; 1932; 1936.

LIBERIA

Askenasy 1888.

LIBYA

Ascherson 1881.
Béguinot 1914.
Borzi 1914; 1917.
De Toni G. B. & Forti 1913; 1914a,b,c; 1916.
Fehér 1936.
Feldmann G. 1946.
Forti 1927; 1928; 1933.
Forti, Marcello & Pampanini 1932.
Gauthier-Lièvre L. 1941b.
Marchesoni 1946; 1947.
Muschler 1910.
Pampanini 1914; 1917.
Pampanini & Maugini 1931.
Rohlfs 1881.

MADAGASCAR

Allen 1938.
Bojer 1837.
Bouriquet 1933.
Bourrelly & Leboime 1946.
Bourrelly & Manguin 1949.
Brunel 1949.
Frémy 1923a; 1926a; 1927; 1930c.
Fritsch 1914.
Groves H. & J. 1887.
Groves J. 1928.
Groves J. & Stephens 1933.
Léandri 1952.
Lefèvre 1927; 1932.
Manguin 1941.
Schmidle 1898.
Skuja 1931.
Van Oye 1923a.
West G. S. 1912c.
West W. & G. S. 1895.
Zaneveld 1939.

MADEIRA & PORTO SANTO

Borge 1911.
Cedercreutz 1941.
Grunow 1870.
Schodduyn 1927.
Zimmerman 1909.

MAURITIUS

Bojer 1837.
Dickie 1875.
Ehrenberg 1854a.
Jadin 1893; 1934.

MORROCO French & Spanish.

Belloc 1895; 1896.
Bellón-Uriarte 1930.
Bornet 1892.
Bourrelly & Gayral 1951; 1954.
Braun-Blanquet & Maire 1924.
Debray 1897.
Feldmann G. 1946; 1953.
Feldmann J. 1946.
Frémy & Burollet 1934.
Gattefossé 1932.
Gattefossé & Werner 1935a,b.
Gauthier-Lièvre H. 1924b; 1925a.
Gauthier-Lièvre L. 1930; 1951.
Gayral 1950; 1954; 1955.
Gayral & Bourrelly 1950.
Gonzalez-Guerrero 1929a,b; 1930; 1931.
Hariot 1909; 1913a,c.
Hy 1913.
Killian & Fehér 1939.
Maire 1924.
Maire & Werner 1934.
Petit 1897.
Schmidle 1899a.
Werner 1934a,b; 1936; 1949.

MOZAMBIQUE

Cholnoky 1952.
Ehrenberg 1848a.
Groves J. 1931.
Hutchinson, Pickford & Schurman 1932.
Peters 1864.
Rich 1932b.
Schmidle 1898.
Zimmerman 1914.

NATAL (including Basutoland).

Bews 1916; 1917.
Fritsch & Rich 1924.
Grove 1894.
Groves J. & Stephens 1926; 1933.
Krauss 1846.
Printz 1921.
Skuja 1931.

NIGERIA & British Cameroons

Ehrenberg 1856.
Hustedt 1943; 1952.
Mills 1932.
Thorold 1952.
Wittrock & Nordstedt 1893.
Wittrock, Nordstedt & Lagerheim 1903.
Zanon 1941a.

NYASALAND

Burkill 1897.
Cunnington 1920.
Dickie 1879.
Müller 1895; 1903; 1904; 1905; 1911.
Schmidle 1899a; 1901a; 1902a,b.
West G. S. 1907; 1912c.

ORANGE FREE STATE

Groves J. & Stephens 1933.
Hutchinson, Pickford & Schurman 1932.
Stephens 1948.

PRINCIPE

Leuduger-Fortmorel 1898.

REUNION

Jadin 1893; 1934.

RHODESIA

Northern

Erlandsson 1928.

Southern

Cholnoky 1954b,d.
Eyles 1916.
Groves J. & Stephens 1926; 1933.
Marloth 1913.
Rich 1935; 1937.
Rich & Pocock 1933.
Rousselet 1944.
Schinz 1906.
West G. S. 1910; 1918.

RODRIGUEZ

Dickie 1877.

SAN THOME

De Toni G. B. 1890.
De Wildeman 1889b.
Hariot 1908.
Henriques 1886.
Leuduger-Fortmorel 1898.

SIERRA LEONE

Leuduger-Fortmorel 1898.
O'Meara 1876.

SOCOTRA

Dickie 1888.
Kitton 1884; 1888.

SOUTH WEST AFRICA

Borge 1899.
Brun 1891.
Dinter 1909; 1918-1929.
Erlandsson 1938.
Esmarch 1911.
Magnus 1890.
Nordstedt 1888; 1900.
Reichelt 1904.
Rich & Pocock 1933.
Schinz 1896.
Vogel 1955.
West G. S. 1912a.

SUDAN

Brook 1952; 1954.
Brook & Rzóska 1954.
Daday 1910b.
Ehrenberg & Hemprich 1831.
Grunow 1870.
Prowse 1954.
Rzóska, Brook & Prowse 1955.
Schweinfurth 1862.

TANGANYIKA incl. Zanzibar, Mafia and Pemba.

Borge 1928.
Cunnington 1920.
Daday 1907; 1910a.
Erlandsson 1928.
Esmarch 1911.
Goebel 1898.
Hieronymus 1895.
Hustedt 1922.
Lemmermann & Jahn 1911.
Müller 1895a,b.

Rendle 1907.
Rich & Pocock 1933.
Ross 1955.
Schmidle 1898; 1900; 1901a, b,c.
Taylor 1932.
Tobler 1917.
Van Meel 1952; 1954.
Woloszynska 1914.

TRANSVAAL incl. Swaziland.

Cholnoky 1953a,b; 1954a,c; 1955b.
Fehér 1936.
Fritsch & Rich 1937.
Groves J. & Stephens 1926.
Hutchinson, Pickford & Schuurman 1932.
Nygaard 1932.
Pocock 1933b; 1937b.
Rich 1932b; 1939.
Rich & Pocock 1933.
Schuurman 1932.
Stephens 1948.
Tempère & Peragallo 1889-1915.

TUNISIA

Barratté 1897.
Belloc 1893; 1895; 1896.
Burollet 1927.
Debray 1897.
Desfontaines 1799.
Feldmann G. 1945; 1946.
Frémy 1926b; 1930a; 1931.
Gauthier-Lièvre H. 1924a,b; 1925a.
Gauthier-Lièvre L. 1931; 1951.
Gayral & Bourrelly 1952.
Hustedt 1953.
Lanzi 1876.
Petit 1897.
Sauvageau 1897.
Serpette 1947; 1948.
Seurat & Frémy 1936; 1937a.
Tempère & Peragallo 1889-1915.

UGANDA

Bachmann 1933; 1936.
Beadle 1932a,b.
Borge 1928.
Borgert 1907.
Cunnington 1920.
Daday 1910a.
De Toni G. B. & Forti 1909.
East African Fisheries 1950; 1951; 1952; 1953; 1954.
Fish 1951.
Ostenfeld 1908; 1909.
Rich 1933.
Ross 1955.
Thomasson 1955.
Virieux 1913.
West G. S. 1907; 1909b; 1910; 1912c.
West W. & G. S. 1896.
Woloszynska 1914.
Worthington 1930; 1932; 1936.

GENERAL

Allorge 1928; 1929.
Bigeard 1934-35.
Borge 1899.
Bornet & Flahault 1886-1888.
Bornet & Thuret 1876-1880.
Bourrelly 1950; 1953.
Braun 1868.
Braun & Nordstedt 1883.
Conrad & Van Meel 1952.
Denis 1926.
Ehrenberg 1843; 1854b.
Frémy 1936.
Fritsch 1907.
Gomont 1892.
Hariot 1889.
Kützing 1849; 1845-71.
Lefèvre 1932.
Lemmermann 1914.
Printz 1940.
Schmidt 1874.
Tiffany 1929; 1930.

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SOME OBSERVATIONS ON THE EFFECTS OF WATER INFLOW AND OUTFLOW ON THE PLANKTON OF SMALL LAKES

BY A. J. BROOK AND W. B. WOODWARD

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SOME OBSERVATIONS ON THE EFFECTS OF WATER INFLOW AND OUTFLOW ON THE PLANKTON OF SMALL LAKES

By A. J. BROOK and W. B. WOODWARD
Brown Trout Research Laboratory, Pitlochry, Scotland

(With 7 Figures in the Text)

INTRODUCTION

Of the factors which determine the abundance of the plankton in a lake it is believed that the flow of water through the lake may at times be of over-riding importance. In fact many small lakes may be regarded as parts of river or stream systems in which the flow of water has been temporarily impeded. Studies of the plankton of flowing waters indicate that the quantity of their plankton is inversely proportional to the current speed (Brook & Rzòska 1954, Rzòska, Brook & Prowse 1955). The magnitude of the influence of the flow of water through a lake will depend on the volume of the lake, the extent of its catchment area and the amount of rainfall on this area. Thus the effect will be greatest in a small shallow lake with a large catchment area receiving high rainfall, and will become less significant the bigger the lake and the smaller the catchment area and rainfall. For purposes of comparison, a figure representing the replacement of water in a lake may be determined by dividing the volume of water contained in the lake by the amount of water passing through for a given period. This *replacement quotient* has been expressed in the following paper in days. Clearly, in any lake an increase in the standing crop of plankton will indicate that the rate of increase of the plankton is greater than the diluting effect of the replacement water, though the converse may not be true, for this may be due to the death of plankton. Hence the productivity of a lake with a rapid replacement of water may actually be greater than that of a lake with a slow replacement though standing crop estimates may suggest the contrary.

The effect of the flow through may, however, be modified by a number of factors. For example, although the annual rainfall on the catchment area is of prime importance, its incidence may also be significant. A short period of heavy rain will have a greater effect than the same amount of rain spread over a longer period. The topography, geology and vegetation of the catchment area will affect the speed of run-off and the proportion of the rainfall that actually runs into the lake. A number of small inlets bringing in the same amount of water as one large inlet may produce a very different result. The effect in lakes with inflowing streams opposite those flowing out will differ considerably from those with inflows near the outflow. Other morphological features of the lake, such as the size and distribution of islands and weed-beds may either confine or spread the inflowing water.

SITES AND METHODS

It has been observed, during the course of observations extending over a period of four years in four Scottish hill lochs, that the population density of the plankton tends to be highest and most stable in lochs with a high replacement quotient.

Table 1. *Some physical data relating to the lochs investigated*

	Volume (cu. ft. $\times 10^6$)	Estimated annual outflow* (cu. ft. $\times 10^6$)	Replacement quotient (days)
Loch Kinardochy	14·0	56·0	91
Loch Moraig	8·9	124·6	26
Loch Choin	18·2	431·0	16
Lochan an Daim	1·1	82·5	5

* This figure was calculated from the size of the catchment area and the annual rainfall at the loch, and was confirmed by measurement of the outflow. The increased amount (2½% per 100 ft) of rain falling on the higher ground around the lochs, and water lost by evaporation have been ignored.

Table 1 gives details of the volume, annual outflow and replacement quotient of these four lochs. The considerable difference in the calculated replacement quotient between Loch Kinardochy and Lochan an Daim will be noted. In view of

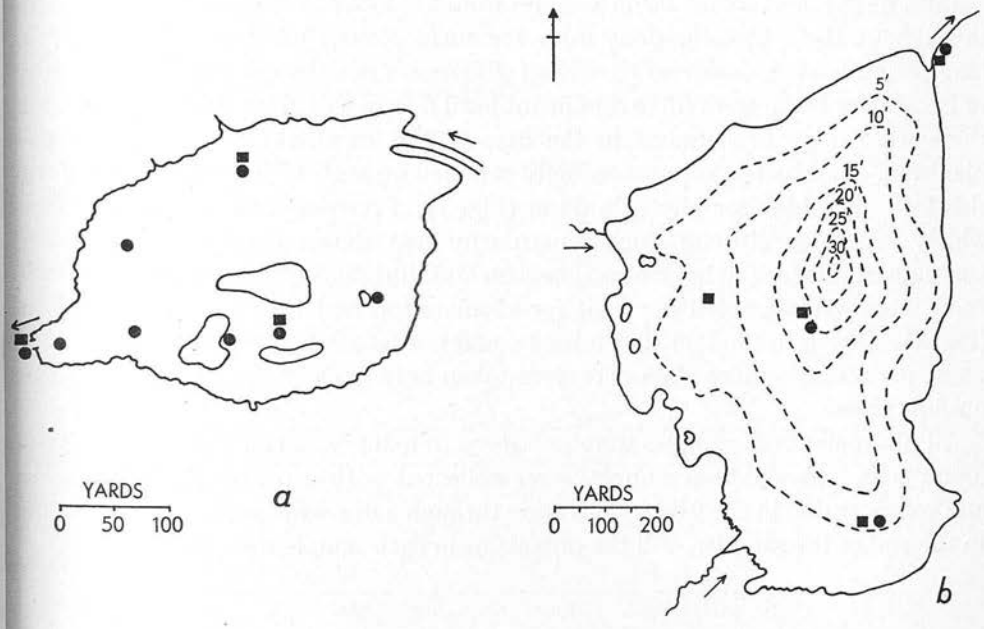

Fig. 1. *a*, Lochan an Daim; *b*, Loch Kinardochy.
Sampling stations: ■, phytoplankton; ●, zooplankton.

these differences detailed concurrent observations were made during the spring and summer of 1954 on the plankton and replacement of water in these two lochs to determine more precisely the influence of flow-through. In Loch Kinardochy (Fig. 1) which is forty-one acres in extent with a maximum depth of 30 ft and average depth of 8 ft, the inflowing water comes from many small drainage

channels. The loch has one small outflow in which a V-notch weir was built to enable accurate measurements of the rate of outflow to be made. Lochan an Daim, an artificial loch, is much smaller and shallower, and is situated some three miles north-west of Loch Kinardochy. It is about ten acres in extent with an average depth of 2½ ft, and maximum depth of 4 ft. It has dense beds of aquatic macrophytes and numerous islands with considerable growths of *Phragmites communis* Trin. and *Carex rostrata* Stokes growing round and on them. There is a well-defined inlet burn which drains a large area of Schiehallion (3547 ft) while at the loch outflow there is a permanent concrete rectangular weir 8 ft in width. A continuous recording depth meter was set up in the loch to record the height of water passing over this weir.

In addition to these studies, measurements of replacement and plankton observations were made at the Pitlochry Reservoirs. These consist of two rectangular basins, the northern holding 1 250 000 gallons and the southern 750 000 gallons. Estimates of replacement in the two basins were determined by measuring the depth of water and current speeds in the inflow pipes. During the periods of observation at both lochs and at the reservoirs plankton samples were taken weekly and, over short periods, daily.

Both phyto- and zooplankton samples from the lochs and reservoirs were taken throughout these investigations from the surface only, previous studies over a long period having shown no significant differences in numbers with depth. Only in Lochan an Daim were there significant local differences in plankton density and these were more pronounced in the case of the zooplankton than for phytoplankton. Eight sites were accordingly sampled on each visit for zooplankton in this loch and three for phytoplankton (Fig. 1). Previous years' sampling of five widely separated sites in Loch Kinardochy had shown plankton distribution throughout this loch to be remarkably even and thus during the present study only three sites were sampled per visit for zooplankton and four for phytoplankton (Fig. 1). Owing to the fact that a boat could not be used on the Pitlochry Reservoirs, plankton samples from here were taken only from the jetty leading to the outflow pipes.

All phytoplankton samples were preserved in iodine and counted in 1 ml Naumann cells. Zooplankton samples were collected with a 5 litre Rodhe sampler and concentrated in the field by filtration through a fine wire gauze which fitted on to the end of the sampler. All the organisms in each sample were counted.

RESULTS OF MEASUREMENTS OF REPLACEMENT QUOTIENT

In Loch Kinardochy water levels fluctuated but little, even after heavy rainfall, and measurements of the rate of flow through indicated that during the period of these observations the replacement quotient varied from seventy days to more than a year (Fig. 2). In Lochan an Daim, however, the depth records show rapid changes in loch height and hence in the volume of the outflow, the replacement quotient varying between one and thirty days (Fig. 3). These changes show

clearly the river-like characteristics of this lochan with its well-defined periods of spate. A typical spate pattern is reproduced from one of the depth recorder charts in Fig. 4.

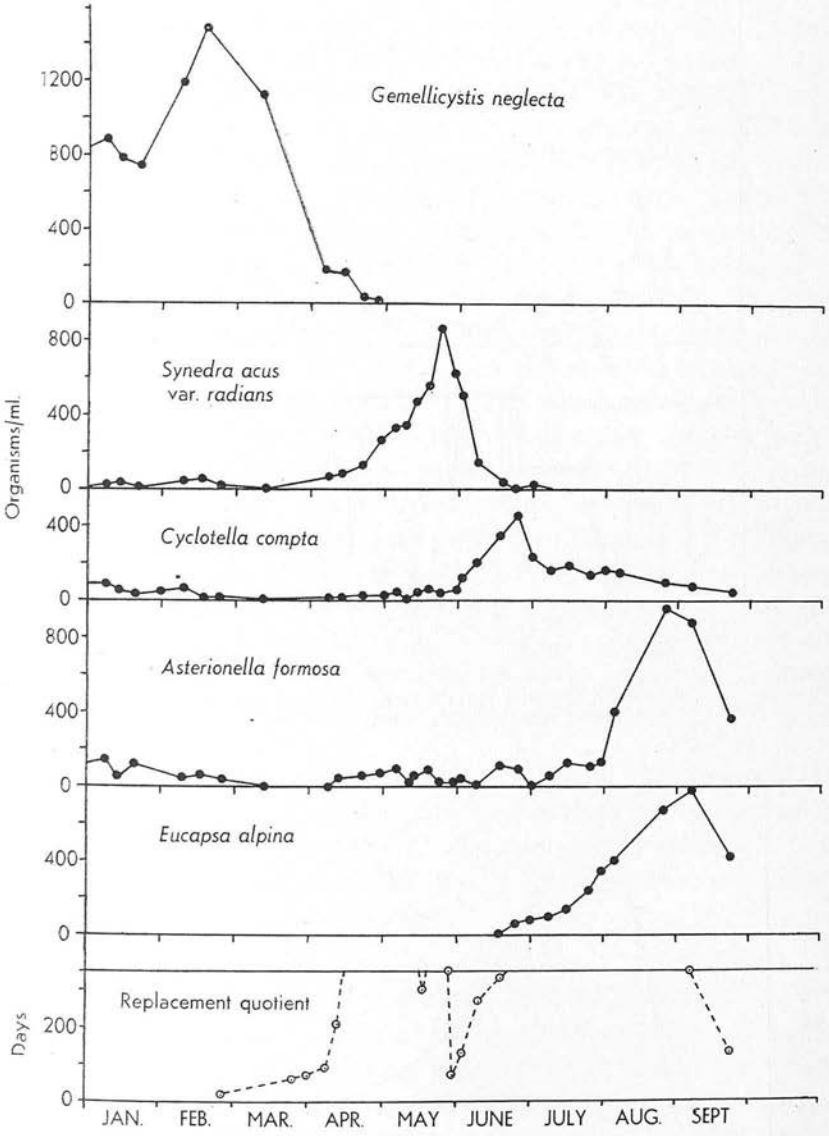

Fig. 2. Loch Kinardochy, 1954: seasonal variations of the principal phytoplankton species and the replacement quotient.

Measurements of the inflows to both basins of the Pitlochry Reservoirs show that their turnover was in general even more rapid than that of Lochan an Daim, their replacement quotient being never more than four days and averaging 2·5 days.

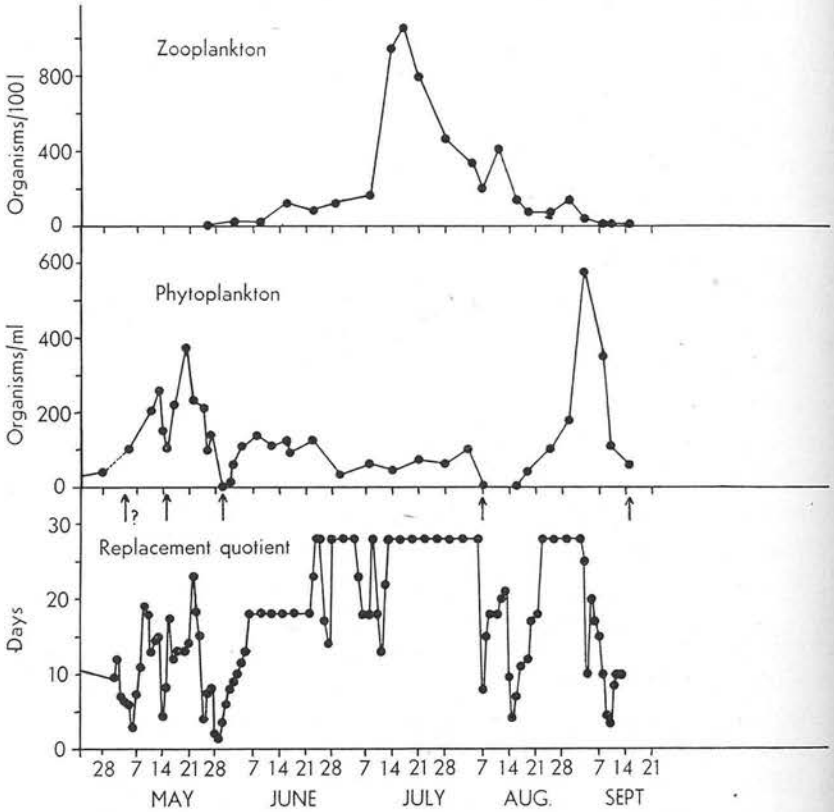

Fig. 3. Lochan an Daim, 1954; seasonal variations in plankton and replacement quotient. Ar indicate spates which affected the plankton.

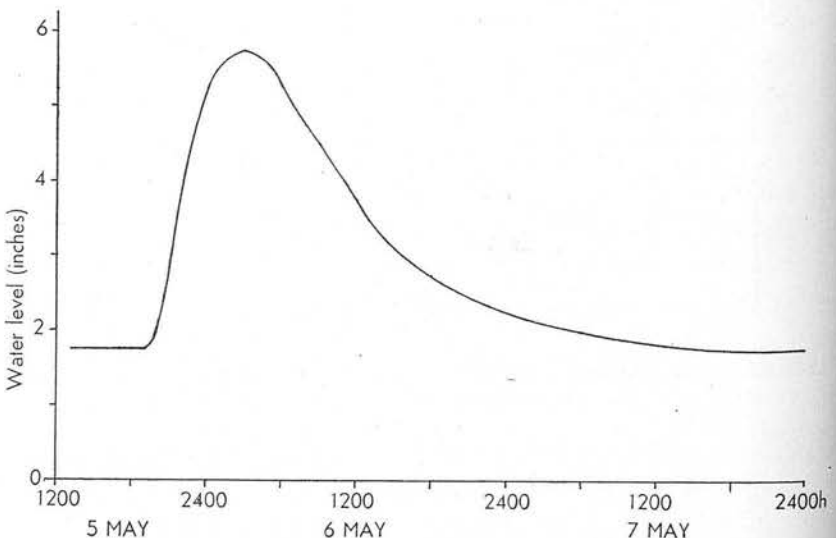

Fig. 4. Spate pattern on the depth recorder chart; Lochan an Daim, 5-7 May 1954

GENERAL BIOLOGICAL RESULTS

The plankton population of Loch Kinardochy is a comparatively stable one in which there is a clear successional pattern of species (Figs. 2, 6 and 7) and at no time have all species been observed to decrease in numbers simultaneously. Moreover, the plankton persists throughout the year in all open water sites, though considered as a whole it is least abundant in winter. Thus in this loch the factors controlling the growth and decline of planktonic organisms would seem to be mainly chemical and biological rather than physical, though of course light and temperature doubtless affect the broader seasonal changes which are observed.

In contrast to Loch Kinardochy there was plankton present in Lochan an Daim for only a comparatively short period of the year, and its appearance, particularly in the case of the zooplankton, seems to be associated with the persistence of a slow flow through, the replacement quotient being consistently greater than eighteen days before the zooplankton developed significantly. In the case of the phytoplankton the situation is less clear though this seems to be able to develop at a lower replacement quotient (probably greater than ten days) and even when conditions are comparatively unstable. Whilst infrequent sampling may have caused the effects of the first recorded spate (between 1 and 6 May) to have been missed, there were clear indications of washouts of phytoplankton following the spates of 14 and 28 May and again on 7 August. The final disappearance of both phyto- and zooplankton began in the first days of September when there was high rainfall which continued throughout that month and the next. During October 1954 there were periods when the estimated replacement quotient was less than one day. Previous years' observations have shown that for a considerable part of each year, usually between October and April, the open water of Lochan an Daim is devoid of plankton.

The consistently low replacement quotient observed in both basins of the Pitlochry Reservoirs seems to confirm that rapid replacement is inimical to plankton production, for throughout the period of observation only occasional plankton organisms were found. It will be remembered that the replacement quotient of both basins was never more than four days.

DETAILED OBSERVATIONS ON THE THE PHYTOPLANKTON

The seasonal changes in the density of the principal components of the phytoplankton of the oligotrophic Loch Kinardochy (see Fig. 2) indicate that the variations observed show no clear association with the variations in the replacement quotient of the loch. The successional pattern of species in the loch is comparable with that of a large, stable loch in which the decline in numbers following a maximum is usually the result of nutrient depletion or, on occasions, parasitism (Canter & Lund 1948, 1951). It is of interest to record in this latter connection that infection by the fungal parasite *Rhizophidium fulgens* Canter probably caused the death in early April of the large *Gemellicystis neglecta* Teiling (Skuja) population which had been present throughout the previous winter.

Unlike Loch Kinardochy, the distribution of phytoplankton in Lochan an Dai shows considerable differences in different localities within the lochan. The phyt plankton first appeared in those areas sheltered by the islands, and throughout t period of its presence it was usually more abundant in these localities than in op water sites. Furthermore, the effects of spates were most devastating to t plankton of the open water which was occasionally removed completely wh some organisms still remained amongst the islands and near weed beds. It seer probable that the replenishment of the open water plankton after such spates w from these localities. Lochan an Daim has an unusual phytoplankton being dor nated by *Dinobryon sociale* var. *americanum* (Brunn.) Bachn., usually from Ap to July and by *Chroomonas acuta* Ütermohl and *Dinobryon sociale* var. *american* from August until its final disappearance in September or October. The plan tonic diatoms *Synedra acus* var. *radians* (Kütz) Hust., *Cyclotella comta* (Eh Kütz., very rare colonies of *Asterionella formosa* Hass. and some Chlorophyce and Cyanophyceae are also present from spring to autumn, but these have nev been recorded in numbers greater than 1 or 2 per ml. It seems possible, sin chemical analyses have shown nothing unusual in the concentration of nutrie in the water of this lochan, that the fuller development of diatoms, Chlorophyce and Cyanophyceae, is prevented initially by the considerable flow of water throu the lochan. By the time this is reduced, their growth and that of *Dinobryon* limited by lack of nutrients, which are taken up by the very dense growths aquatic macrophytes and associated algal epiphytes that develop in early summ Thus it seems that only rapidly reproducing species and possibly only species w low nutritional requirements can succeed in lochs with low replacement quotien In this connection it is of considerable interest to compare the phytoplankton Lochan an Daim with that of Loch Moraig which, though chemically and b logically similar, has a much higher replacement quotient (Table 1 and Fig. Although the same species of phytoplankton are present in both, only in L Moraig with its higher replacement quotient does a complete plankton spectru with periods of diatom and cyanophycean dominance, in addition to the consid able maxima of *Dinobryon* and *Chroomonas*, develop. Observations in 1953 (Fig showed that the maxima of *Dinobryon* in both lochs occurred in late April, bu Lochan an Daim it appeared much later and disappeared sooner than in L Moraig. Furthermore in Loch Moraig its decline was accompanied by an incre in the population density of *Synedra acus* var. *radians*, to be followed later *Cyclotella* spp. Thus it may be said that differences in the rate of replacem produce qualitative as well as quantitative differences in the plankton.

DETAILED OBSERVATIONS ON THE ZOOPLANKTON

In the Pitlochry Reservoirs the only planktonic crustacean present was *Daphn hyalina* var. *lacustris* Leydig and this variety occurred spasmodically and only very small numbers.

The zooplankton of Lochan an Daim is dominated by *D. hyalina* var. *lacust*

with *Diaphanosoma brachyurum* (Liéven) appearing in small numbers later in the year. Though *Daphnia* was first found to be present on 26 May (see Figs. 3 and 7), it did not become numerous until 14 July and attained its maximum density of 1300 individuals/100 l. three days later, on 17 July. This maximum consisted

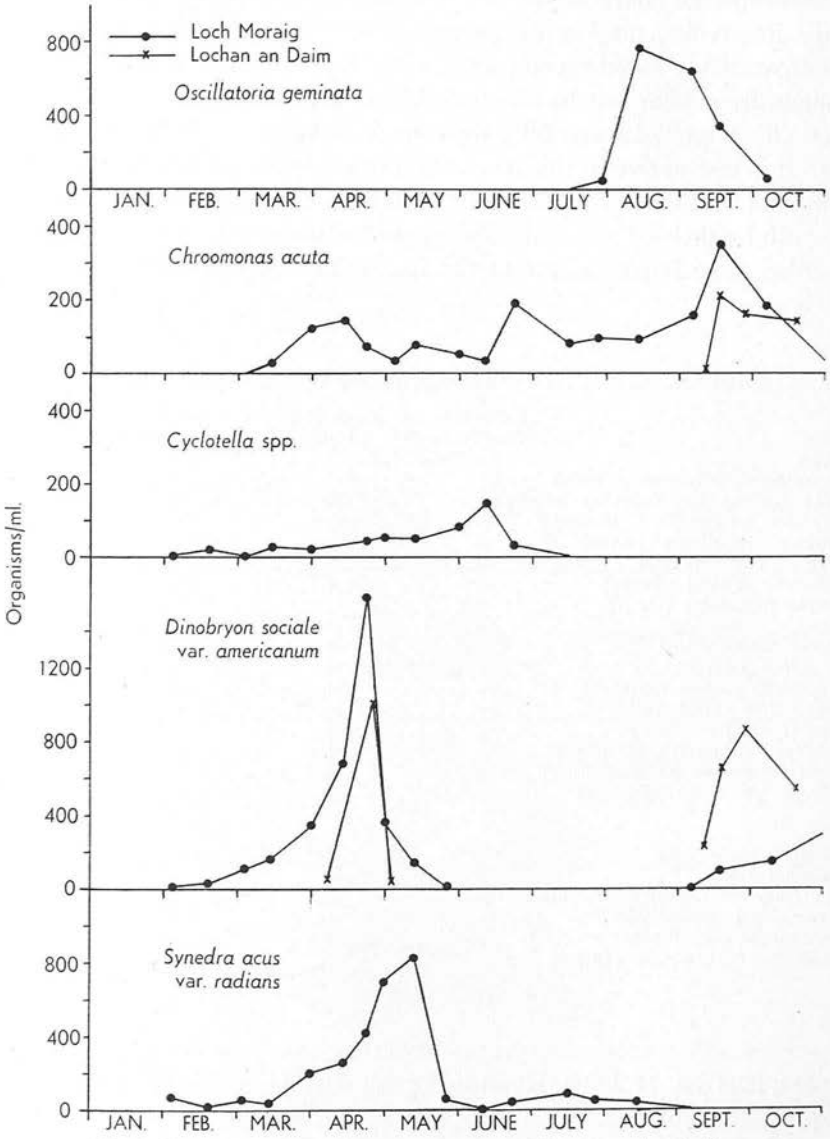

Fig. 5. Loch Moraig and Lochan an Daim, 1953: seasonal variations of the principal phytoplankton species.

almost entirely of young stages which reached maturity, with the appearance of ovigerous female adults and further young stages, some two to three weeks later. There were indications early in August that, as in previous years, a second maximum was about to be produced. However, a period of high water levels ensued

and only small numbers appeared. The period of higher replacement quotie which followed this apparent washout produced a small, short-lived increase i numbers which included a proportion of ephippial females. Finally, further hi water levels in the middle of September removed all save occasional individua

The monospecific character of the zooplankton of Lochan an Daim (and t Pitlochry Reservoirs) may as in the case of the phytoplankton be the result their comparatively rapid replacement, since Loch Moraig, which is biological and chemically similar but has a much higher replacement quotient, has a zo plankton characterized when fully developed by large numbers of *Daphnia* a *Cyclops*. It is instructive in this connection to compare the species list of Loch an Daim with that for Loch Moraig (see Table 2). Although most species are co mon to both localities it seems significant that only occasionally do individuals species other than *Daphnia hyalina* var. *lacustris* occur in Lochan an Daim.

Table 2. *List of zooplankton from the localities mentioned in text*

	Pitlochry Reservoirs	Lochan an Daim	Loch Kinardochy	Loch Moraig
CLADOCERA				
Diaphanosoma brachyurum (Liéven)	−	+	−	−
Daphnia hyalina var. *lacustris* Leydig	+	+	+	+
Simocephalus vetulus (O. F. Müller)	−	+	−	+
Ceriodaphnia reticulata (Jurine)	−	+	−	+
Bosmina obtusirostris Sars	+	+	+	+
Drepanothrix dentata (Eurén)	+	+	−	−
Eurycercus lamellatus (O. F. Müller)	−	+	−	+
Acroperus harpae Baird	+	+	−	+
Alona affinis (Leydig)	+	+	+	+
Rhynchotalona falcata (Sars)	−	+	+	+
Alonella excisa (Fischer)	−	+	−	+
A. nana (Baird.)	+	+	−	+
Peracantha truncata (O. F. Müller)	−	+	−	+
Chydorus sphaericus (O. F. Müller)	+	+	−	+
Polyphemus pediculus (Linneus)	+	+	−	+
COPEPODA				
Diaptomus gracilis Sars	+	+	+	−
Canthocamptus spp.	+	+	+	+
Cyclops (*Eucyclops*) *agilis* Koch, Sars	−	+	−	−
C. (*Paracyclops*) *affinis* Sars	−	+	+	−
C. (*Cyclops*) *strenuus* Fischer	+	+	+	+
C. (*Acanthocyclops*) *viridis* (Jurine)	−	+	−	+
Totals	11	21	8	16

The zooplankton of Loch Kinardochy consists of a *Diaptomus-Cyclops-B mina-Daphnia* complex in which copepods appear before Cladocera, though t latter remain later in the year. Figs. 6 and 7 show the changes in the abundan of the principal zooplankton species during the period covered by the prese observations. It is of interest to compare the development of the *Daphnia* popul tion in Kinardochy with that of Lochan an Daim (Fig. 7). It will be noted th although *Daphnia* was found in both lochs at approximately the same time, i first maximum was recorded in Loch Kinardochy on 16 June. In Lochan a

Daim, however, it did not occur until a month later, on 17 July, despite the apparent lack of competition from other species.

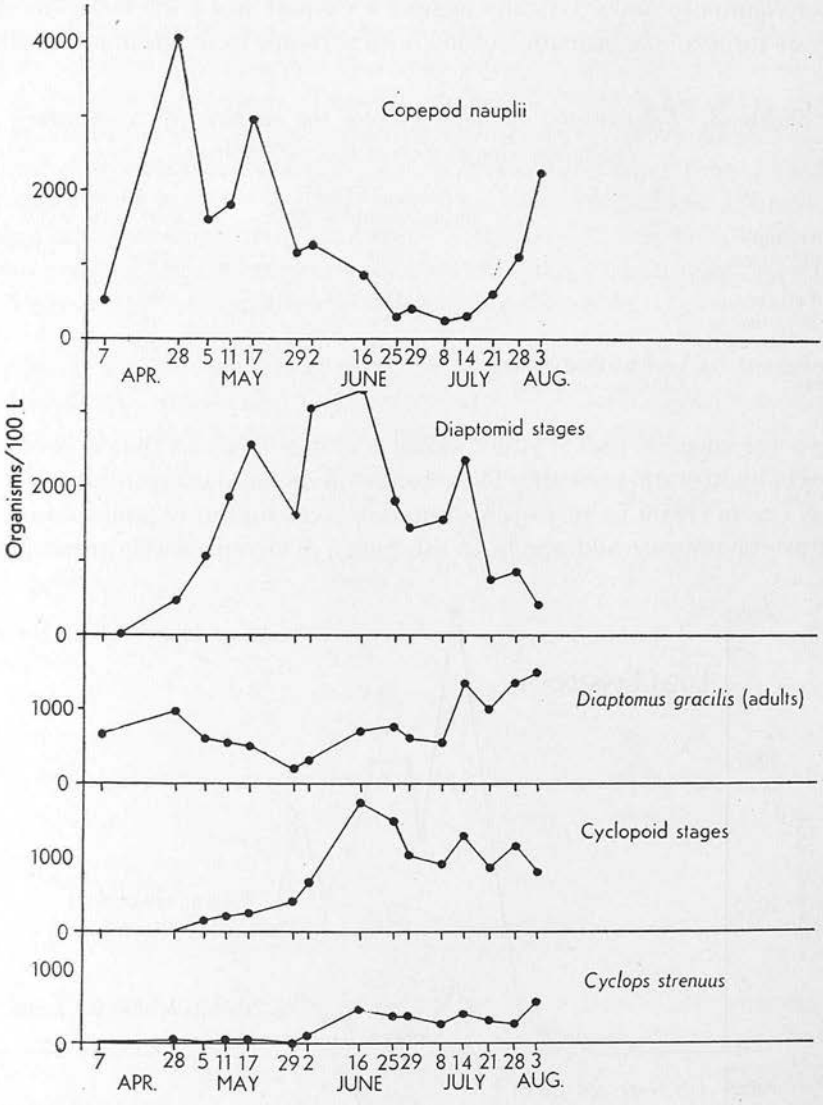

Fig. 6. The copepod zooplankton of Loch Kinardochy, 1954 (average of three sites).

Some consideration has been given, both in Loch Kinardochy and Lochan an Daim, to the effectiveness with which different species and age-groups of the same species can avoid being carried down the outflow (Table 3). It is apparent from this table that any losses which might be due to water replacement in Loch Kinardochy will be greatly reduced by the apparent rheotactic responses shown by these organisms in evading the draw down the outflow. It is clear that for each species success in evading the outflow increases with age, though it has been observed that adults in a senile condition do not show marked evasive responses.

Laboratory observations in an experimental trough have shown that, where Cladocera swim steadily and continuously against a current, copepods only beg to swim vigorously and erratically against a current when the latter accelerat rapidly as for example near the outflow. An attempt to determine the nature

Table 3. *Effectiveness of avoidance of the outflow by zooplankton*

The figures show numbers present per 100 litres

	Average of all outflow samples (A)	Average of all samples from site near outflow (B)	Ratio B/A
Copepod nauplii	525	1330	2·5
Diaptomid stages	300	1286	4·3
Diaptomus gracilis	77	711	9·2
Cyclopid stages	145	590	4·0
Cyclops strenuus	14	167	11·9
Bosmina obtusirostris	128	1809	14·1
Daphnia hyalina var. *lacustris* — Loch Kinardochy	20	275	13·8
Daphnia hyalina var. *lacustris* — Lochan an Daim	90	80	0·9

this response suggests that it is not visual and it is believed that it is related changes in hydrostatic pressure. The recent experimental observations of Knigh Jones & Qasim (1955) on responses of marine zooplankton organisms to chang in hydrostatic pressure add weight to this belief. The remarkable anomaly show

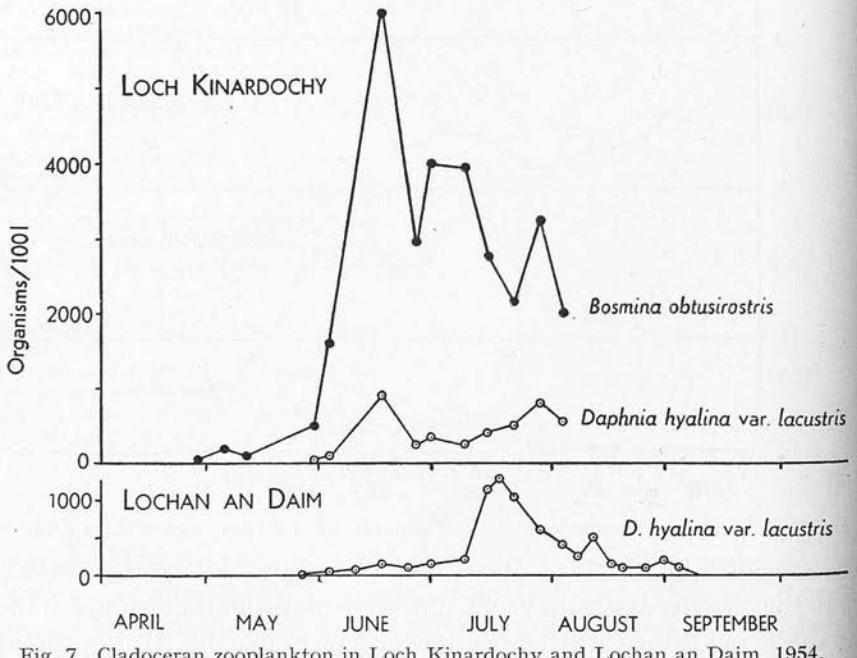

Fig. 7. Cladoceran zooplankton in Loch Kinardochy and Lochan an Daim, 1954.

by the figures in Table 3 for *Daphnia* in the two lochs may possibly be explain by the differences in their width and contour, there being a much greater chan of successfully evading a shallow, narrow outflow (as in Loch Kinardochy) th a broad deep one as at Lochan an Daim.

DISCUSSION

In the sea and in large lakes, the standing crop of plankton is usually taken as a measure of productivity. It has been tacitly accepted that a measure of the standing crop also gives an indication of the productivity of small lakes. The present results, however, seem to suggest that such estimates may be of little value and can even be very misleading. Detailed studies of communities other than the plankton and of the chemical characteristics of the four Scottish hill lochs already mentioned show strikingly how misleading such results can be. From a consideration of these biotic and chemical characteristics these lochs can be arranged in an ascending order of productivity as shown in Table 4. It will be noted from this table that, in terms of bottom fauna, Lochan an Daim is about three times as rich as Loch Kinardochy, in addition to being richer chemically. Comparisons of the

Table 4. *The productivity of four Scottish hill lochs in terms of submerged macrophytes, quantitative evaluation of the bottom fauna, chemical characteristics, and average zooplankton density*

	Loch Choin	Loch Kinardochy	Lochan an Daim	Loch Moraig
Replacement quotient	16	91	5	26
Indicator macrophytes	*Littorella*, *Lobelia*	*Littorella*, *Lobelia*	*Potamogeton natans*; some charophytes	*P. natans*; abundant charophytes
Bottom fauna per sq. ft { numbers	33	38	110	264
Bottom fauna per sq. ft { weight (g)	0·076	0·141	0·324	0·572
pH	6·14-7·52	6·80-7·67	7·22-8·08	7·38-8·13
Alkalinity (p.p.m. $CaCO_3$)	1·6-7·8	11·0-29·0	23.0-52·8	35·8-85·6
Free ammonia (p.p.m.)	0·168-0·756	0·103-0·636	0·974-1·240	0·095-1·200
Silica (p.p.m. SiO_2)	0·55-2·14	0·49-2·28	1·30-3·35	0·41-4·72
Zooplankton: average per visit (1950-52) per 100 l.	562	2790*	108	1211

* The 1952 figure for Loch Kinardochy. Figures for 1950 and 1951 are not included since they show the effects of treatment with rotenone in 1949-50 to eradicate pike.

phytoplankton and zooplankton estimates for these two lochs, however, show Loch Kinardochy to be very much richer than Lochan an Daim (Figs. 2, 3, 6, 7) and emphasize how erroneous productivity estimates based on the standing crop of plankton can be.

The above considerations would seem to suggest that quite erroneous estimates of the plankton productivity of lakes may be obtained if these are sampled without reference to the important physical factor of replacement. Moreover, the present results emphasize that, particularly in lakes with a low replacement quotient, sampling should be carried out at frequent intervals. It is also clear that, since changes in water level occur so rapidly (see Fig. 4), the full extent of replacement can only be assessed if continuous records of outflow are available. In view of this it is suggested that the productivity of such lakes can be best assessed by the study

and measurement of abundance of communities of plants and animals more stab than the plankton (e.g. bottom fauna, attached algal communities, etc.) which a not directly affected by the changes in the rate at which water is flowing throu the loch.

It is of interest to note that Ruttner (1940) had drawn attention to the impo tance of the relationship between inflow and outflow in Alpine lakes. He states th it is this factor which brings about the spring and early summer population minir of almost all plankton species in such lakes despite their rate of reproduction bei high during these periods owing to favourable environmental conditions. Mo recently Lund (1954, p. 172) has stressed the importance of winter floods in relati to the abundance and periodicity of the plankton diatom *Melosira italica* subs *subarctica* O. Müll. Their effects were particularly noticeable in Esthwaite Wat and Blelham Tarn where the replacement time is relatively short. Decreases the population of this diatom in these lakes, when growth is slow in winter, we on occasions found to be considerable.

Bearing in mind the effects of replacement, it is of interest to consider th increased plankton production which is sometimes observed in lakes where th water level has been raised. While such increases may have been in part due decay in the inundated areas, it is clearly possible that the appearance of larg amounts of plankton could also be due to a reduction in replacement quotient d to the raising of the water level, although the volume of water passing through th lake has remained unchanged.

ACKNOWLEDGMENTS

The authors are indebted to Mr A. V. Holden and Mr N. C. Morgan for pr viding, respectively, the chemical data and quantitative information on the bott fauna which appears in Table 4; also to Mr K. A. Pyefinch for helpful advice the preparation of this paper.

SUMMARY

1. Four years' observations on the plankton populations of four Scottish l lochs have shown that their density tends to be highest and that they are m stable in lochs with a low rate of water replacement.

2. Detailed studies were made during the spring and summer of 1954 on t plankton and replacement of water in one of these lochs having a low rate replacement and in another with a high rate in order to determine more precis the influence of this factor.

3. These studies indicated that at times the rate of replacement may be a fac of over-riding importance and may produce not only quantitative but a qualitative differences in the plankton.

4. Some observations have been made on the effectiveness with which differ species and age-groups of individual species of zooplankton can avoid be carried down the outflows of lochs.

5. The results of this investigation indicate that the standing crop of plankton cannot be used as a measure of the productivity of small lakes, particularly where the replacement of water may be considerable.

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17

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I. Loch Kinardochy

By A. J. BROOK, B.Sc., Ph.D., F.L.S. and A. V. HOLDEN, B.A

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Fertilization Experiments in Scottish Freshwater Lochs

I. Loch Kinardochy

INTRODUCTION

As part of a programme of investigations into the factors affecting the biological productivity of Scottish freshwater lochs, and of the means of increasing this productivity, several experiments involving the addition of various types of mineral fertilizers have been carried out. The literature on this topic has been reviewed by Mortimer and Hickling (1954), who deal mainly with fertilizers in fish ponds and by Maciolek (1954) who gives some attention to the fertilization of lakes.

The present report describes the first experiment of a series which is being carried out in Scotland. This initial experiment has provided information on the extent to which a single addition of fertilizer can affect parts of the flora and fauna, and the period for which these effects can be expected to continue. Most of the results relate to the chemical and botanical changes observed, though some effects of artificial enrichment on the bottom fauna have also been recorded. No study of the fish population (pike, *Esox lucius* L.) was made, as the numbers had been depleted by the application of derris extract to the loch in 1949 and 1950.

DESCRIPTION OF LOCH KINARDOCHY

Loch Kinardochy (Nat. Grid Ref. 27/776552), a small hill loch in north-west Perthshire, lies to the south-west of Loch Tummel into which it drains. It is roughly triangular in shape (see Fig. 1), with a single outflow at the northern end, and six small inlet streams, which in dry weather supply little or no water to the loch. Two enter the west bay and four flow into the south bay, although one stream, the largest, has two outlets into the loch. The area of the loch is 41 acres (16·6 ha.), the maximum depth 30 feet (9·2 m.) and the mean depth has been estimated as 8·9 feet (2·7 m.). The loch is situated 1170 feet (360 m.) above mean sea level, and the surrounding land is gently-sloping peat moor, with an area of marshy ground to the south-east.

Although the maximum depth is 30 feet, the circulation of the water, due mainly to wind action, is such that no stable thermocline is present during the summer months. The largest temperature difference recorded in 1952 between surface and bottom layers was 3·1°C,the difference between four and six metres depth being 1·9°C. These conditions existed for a period of five days during calm weather, but no chemical stratification was observed. Subsequently, this temperature gradient disappeared completely as the result of a gale.

The shore of the loch is stony except in the south bay and the regions near the outlet and the mouths of the inflowing streams, where sand is the main deposit, while at one point on the eastern shore there is a partly submerged limestone outcrop. The bottom deposit, beyond the stones or sand, is a fine black mud, mostly inorganic in composition.

The littoral aquatic flora is generally sparse, for much of the shore, particularly at the northern end, is subjected to considerable wave action, and the only phanerogams here are occasional plants of *Littorella uniflora* and, very rarely, *Lobelia dortmanna*, growing among the sparse inorganic silt. At the more sheltered southern end, *Lobelia* is more abundant, and between depths of two and five feet is frequently intermingled with extensive beds of *Myriophyllum spicatum*. Also at the southern end of the loch, but in deeper water, is a large bed of *Potamogeton praelongus*, while at the northern end only scattered plants of this species occur. A fairly extensive bed of *P. gramineus* also grows in the southern bay of the loch though in shallower water than *P. praelongus*. An extensive bed of *Equisetum fluviatile* grows out from the mouth of the inflowing burn near the south-western shore, and in each of the small bays on this shore there are stands of *Carex rostrata*.

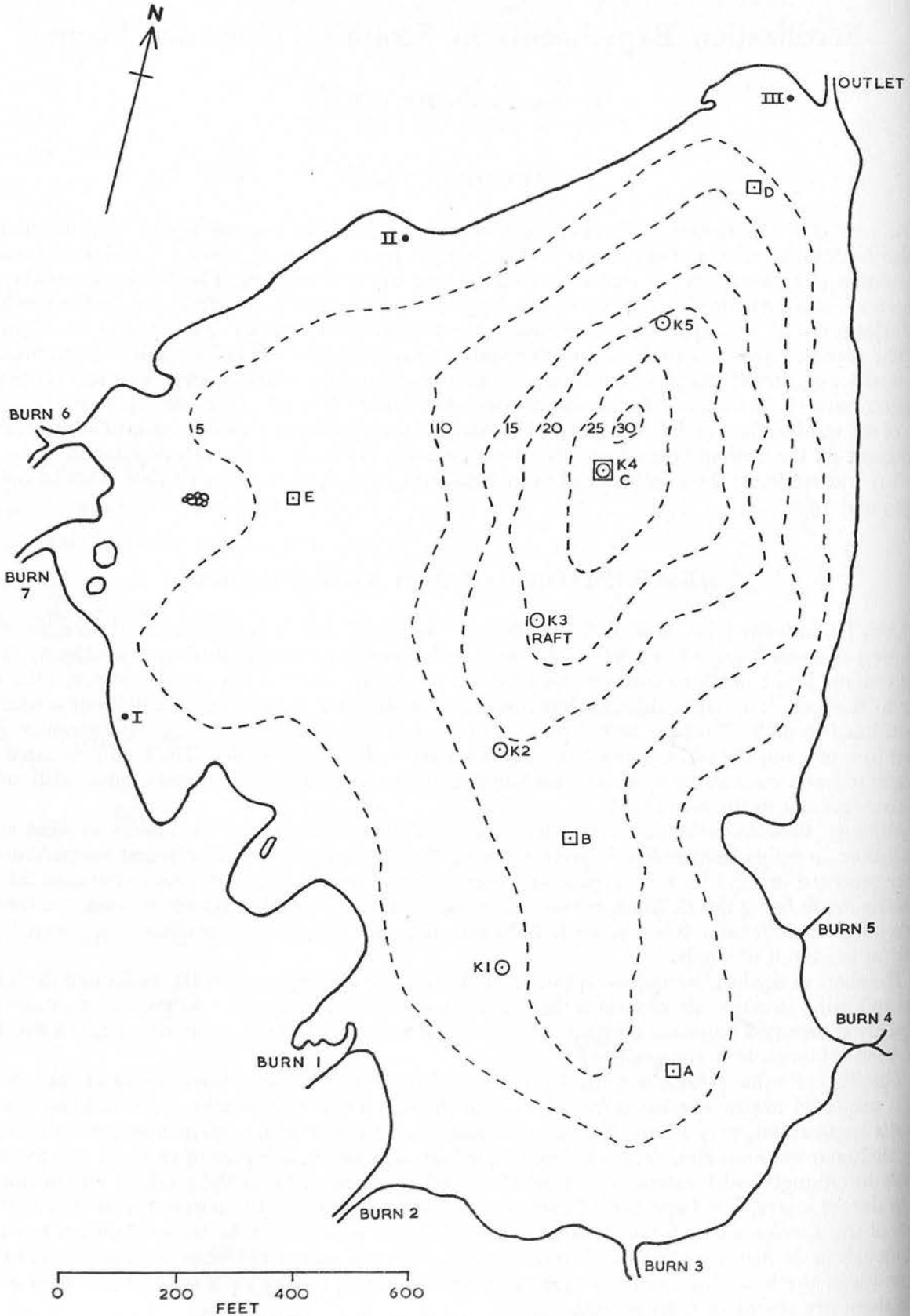


Fig. 1. Loch Kinardochy. showing depth contours and sampling sites

⊙ K1–K5 Chemical samples and Ekman grab samples.
● I – III Bottom fauna tray samples.
▣ A – E Phytoplankton samples.
– – – – Depth contours at five feet intervals.

Details of the composition of the phytoplankton of the loch before and after its fertilization are given in the botanical section of this report (p. 18). The zooplankton consists of a *Diaptomus-Cyclops-Bosmina-Daphnia* complex in which copepods appear before cladocerans, though the latter remain later in the year. A list of the zooplankton of the loch (exclusive of rotifers) can be found in Brook and Woodward (1956, p. 30).

An outstanding feature of the bottom fauna is the large number of *Gammarus lacustris*. Where the littoral is stony, this amphipod and *Planorbis contortus* are permanent and commonly occuring members of the fauna. *Ecdyonurus dispar*, *Leptophlebia marginata*, *Capnia atra*, *Chloroperla torrentum* and chironomid larvae are common seasonally. Along the sandy shores the fauna is sparse except for *Gammarus lacustris* and the seasonal occurrence of the nymphs of *Leptophlebia marginata*. In deeper water, where the bottom is muddy, the most abundant invertebrates are chironomid larvae, *Pisidium nitidum* and *P. hibernicum*. *Gammarus lacustris* is frequent down to a depth of 12 feet, and it is also present at greater depths.

The fish population consists of pike which feed mainly on bottom fauna, although the larger pike also prey to some extent on young fish of their own kind.

APPLICATION OF THE FERTILIZER

On 14th July 1952 two tons (2032 kg.) of calcium superphosphate in powdered form were added to the loch. Distribution was effected by trailing 140 lb. bags, opened at one corner, over the stern of a small boat propelled by an outboard motor. The propellor assisted to some extent in dispersing the fertilizer, but in shallow water a considerable proportion appeared to fall directly to the bottom. The surface water temperature at the time was 15·3°C.

Errors in the uniformity of distribution over the loch were minimised by sub-dividing the loch surface into sections marked by buoys and fixed points on the shore, and allocating the appropriate weight of fertilizer to each section, on the basis of 1 cwt. per acre of surface area (125·6 kg./ha.). The application took three hours, and the uniformity of distribution was examined subsequently by estimating the soluble phosphate in water samples taken at various depths at marked sampling sites, and at additional points on the surface. The results of these analyses are discussed later.

METHODS OF CHEMICAL ANALYSIS

Samples of water for analysis were taken in polythene bottles, fitted with polythene caps, the samples below the surface being obtained with the aid of a Casella water sampler, normally used for bacteriological or dissolved oxygen examinations. Unfiltered aliquots were used for total phosphorus analyses, and for the determination of pH and alkalinity. For all other analyses, the samples were filtered through a No. 541 Whatman filter paper to remove plankton and detritus, the first portion of the filtrate being rejected. As far as possible, all analyses were carried out within 24 hours of sampling. The results quoted in this report, except in the section on phosphate distribution, are in general the means of several samples taken at different points in the loch. The following methods of analysis were used.

pH and Alkalinity A 'Cambridge' pH meter, with glass and calomel electrodes, was used. After the determination of pH, the 50 ml. aliquot was titrated with 0·02N sulphuric acid to pH 5·00 to determine the bicarbonate alkalinity. (This value, expressed as parts per million of calcium carbonate, is given by ml. 0·02N sulphuric acid × 20.)

Calcium The method of Walker and Murtagh (1951), employing a titration with sodium versenate, was used, the results being expressed as p.p.m. calcium carbonate.

Ammonia and Nitrate The methods given in the handbook of the American Public Health Association (1946, pp. 67 and 69) were used. Ammonia was determined by direct Nesslerisation of a 50 ml. aliquot, and nitrate by the phenoldisulphonic acid method. Determinations of the colour intensity developed

were made on a Hilger 'Spekker' absorptiometer, using a 4 cm. cell and Ilford 601 filters. Reagent blanks and standards were carried with each set of samples, and sample blanks measured before colour development in all cases except that of nitrate.

Silica Soluble silica was estimated by the following modified form of the method described by Robinson and Thompson (1948a). 50 ml. aliquots were treated with 0·25 ml. of 6N sulphuric acid and allowed to stand not less than ten minutes before reading the sample blanks. This allows for the partial decolorisation of the natural yellow colour of the water resulting from the use of an acid reagent. 0·5 ml. of 10% ammonium molybdate solution was then added, and the final colour intensity measured after ten minutes. The silica concentrations corresponding to both measurements are read from a graph based on determinations using standard potassium chromate solutions (A.P.H.A. Handbook, 1946, p. 45) and the difference gives the soluble silica concentration. Measurements were made on the 'Spekker' absorptiometer, using Ilford 601 filters and a 4 cm. cell.

Inorganic Phosphate Soluble inorganic phosphate was estimated by the method of Robinson and Thompson (1948b), the colour intensity being measured after 15 minutes. The colour intensity was measured on the 'Spekker' absorptiometer, using Ilford 608 filters, and a 4 cm. cell. When the phosphate concentration was very low, a 20 cm. cell was used.

Total Phosphorus For the determination of total phosphorus, unfiltered samples were used. The phosphorus thus estimated includes that in plankton and detritus, soluble organic compounds and dissolved inorganic phosphate. 50 ml. aliquots were evaporated with 0·2 ml. of 60% AR perchloric acid on an electric hotplate, the surface temperature of which was just insufficient to cause boiling of the contents. Heating was stopped when the concentrates began to evolve white fumes of perchloric acid. After cooling, diluting with distilled water, heating to convert pyro- and meta-phosphates to ortho-phosphate, and adjusting the pH to 4·0, the volumes were made up to 50 ml. Phosphorus was then determined as inorganic phosphate by the method previously quoted. The standard deviation of a single determination by the method described was $\pm 5\mu$g. phosphorus per litre. Unfortunately this method was not brought into use until 8th August, 1952. Most values obtained prior to this date were unreliable, except where special precautions were taken to avoid overheating during the perchloric acid digestion. Only the reliable results are quoted in this report.

CHEMICAL CHANGES FOLLOWING FERTILIZATION

Phosphorus In view of the somewhat meagre information available in the literature concerning the disappearance of added phosphate following fertilization operations, the opportunity was taken of studying in detail the distribution of phosphate throughout the water mass, and the subsequent decline in concentration. As mentioned elsewhere, no stable thermocline has been recorded during the summer months in Loch Kinardochy, the prevalence of wind being the most probable reason. The rapidity with which the concentration of phosphate became uniform throughout the loch, as described below, confirms that there is a considerable degree of circulation at all depths, even under the influence of only light winds.

One hour after the distribution of fertilizer was completed, a series of water samples was taken at various points over the water surface, and at two sampling sites K1 and K4 (see Fig. 1) samples were taken at a series of different depths. After two hours, twenty hours, and two days, the sampling was repeated. The analyses for soluble phosphate phosphorus are presented in Table 1, and indicate the rapidity with which the water circulation distributed the phosphate. Owing to a slight bias in the initial distribution of the fertilizer as a result of its application by units of area rather than volume, the concentrations at K1 (in the shallower zone) were initially higher than those of comparable depths at K4 in the deeper zone, but after two days this difference had disappeared.

Further series of samples were taken on succeeding days to examine the phosphate distribution both horizontally and vertically, the latter at K4. The standard deviations of the mean of the surface samples and also of the vertical series of samples at K4, were calculated, and the results are given in Table

TABLE 1

Phosphate Concentrations (μg. P/litre) at various Depths, after Fertilization

	Station K1			Station K4								
	0m.	1m.	2m.	0m.	1m.	2m.	3m.	4m.	5m.	6m.	7m.	8m.
1 hour after ..	440	395	320	265	175	220	245	285	385	505	—	—
2 hours after ..	295	296	338	238	—	269	—	210	—	464	—	340
20 hours after ..	332	334	371	269	286	280	294	277	280	282	278	262
44 hours after ..	284	—	278	310	304	302	—	294	296	327	319	306

— No sample

TABLE 2

Horizontal and Vertical Distribution of Phosphate after Fertilization

Period after Fertilization (days)	Mean Surface Concentration (μg. P/litre)	No. of Samples	Standard Deviation of Mean (μg. P/litre)	Mean Sub-Surface Concentration (μg. P/litre)[1]	No. of Samples	Standard Deviation of Mean (μg. P/litre)
1	319	12	±21	278	9	±5
2	298	16	±14	304	9	±9
4	283	7	±16	286	5	±5
6	252	5	±14	264	5	±5
8	244	6	±14	254	5	±5
10	233	7	± 7	240	5	±8
12	206	5	± 6	210	5	±6
16	178	6	± 4	180	5	±3

[1] Station K4

These figures demonstrate how quickly the phosphate became uniformly distributed. This was presumably due to the continual circulation of water, which must be a major factor in the supply of other nutrients to the flora.

Sampling was continued until the soluble inorganic phosphate concentration had fallen below the limit of detection, the frequency of sampling being reduced until samples were being taken once weekly at four widely-spaced surface positions. Close agreement between the four samples was obtained in all cases. In addition, occasional vertical series were also taken at various points, particularly at K4 (maximum depth 8m.), but no significant variation of phosphate concentration with depth was found. Samples taken within beds of *Equisetum fluviatile*, *Carex rostrata* and *Potamogeton praelongus* never consistently exhibited concentrations of phosphate lower than those in the open water of the loch.

The course of the decline in concentration of the phosphate is illustrated in Fig. 2. As this curve is of an exponential form, the logarithm of the concentration has also been plotted against a linear time scale. During the first 31 days, the decline in concentration appears to have been rather more rapid than in the subsequent period, but even when the complete period of 105 days is considered, the results can be represented by a straight line, the correlation coefficient being −0·996. The rate of loss of phosphorus, calculated from the data for the complete period of 105 days, is 27·1 μg./litre per mg./litre per day, or 2·71% of the concentration per day. The rather more rapid decrease during the first 31 days is equivalent to 3·42% per day. The exponential decline appears to have been maintained despite the many factors which must have been involved. These are discussed in more detail later.

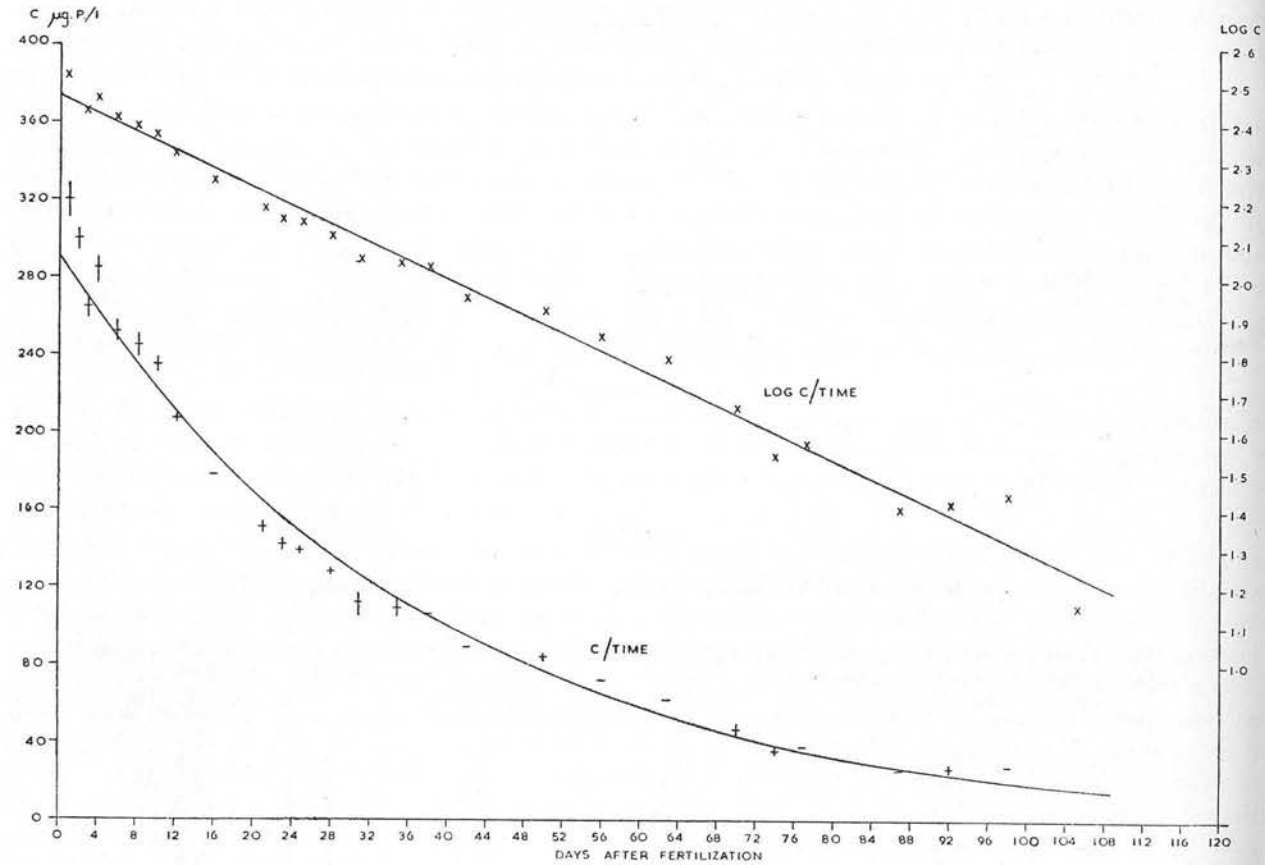


Fig. 2. Decrease of concentration of soluble phosphate after fertilization (vertical lines represent standard error of mean of each group of samples).

The total weight of superphosphate added to the loch was two tons (2032 kg.), and the fraction of water-soluble phosphorus was 7·3% (16·7% P_2O_5). The volume of the loch at the time of fertilization was estimated to be 324 acre-feet ($4{\cdot}0 \times 10^8$ litres). The theoretical concentration of phosphate phosphorus, assuming complete solution, is 370 μg./litre, and the concentration estimated by extrapolation from Fig. 2 is about 330 μg./litre, or 90% of the former value.

Measurements of the total phosphorus content of the water, including that contained in plankton and in soluble organic compounds, were made frequently. For this analysis, any large zooplankton organisms present in the samples were removed by filtration through a 50-mesh plankton net. The differences between the total phosphorus and soluble phosphate phosphorus concentrations were recorded as organic phosphorus. The initial concentration, prior to fertilization, was 14 μg. P per litre, and the highest value recorded subsequently, on the 28th and 98th days, was 27 μg. P per litre.

Analyses were also made for pH, bicarbonate alkalinity, calcium, nitrate, ammonia and soluble silica. Except in certain instances, no abnormal changes occurred in the concentrations of these constituents but such changes as did occur must be assessed in relation to the normal seasonal variation to be expected. The various analyses are discussed individually below. Observations were made in detail up to the end of 1953.

pH The pH in 1951, the year before fertilization, rose from 7·3 at the time of the disappearance of ice-cover in April, to over 7·7 in August, and declined to below 7·2 in December, when ice again covered the loch. Temporary fluctuations occurred throughout 1951 and 1952, and were more noticeable in 1952 due to the higher frequency of sampling. High values of pH were not correlated with maximal concentrations of phytoplankton at any time. The maximum recorded pH in 1952 was 7·9 in August,

but as other lochs in the area also had higher pH values at this time than in the same period in 1951, the increase cannot be associated with the greater post-fertilization photosynthetic activity.

Bicarbonate alkalinity In 1951 the bicarbonate alkalinity rose steadily throughout the spring and summer from 21 mg./l. to 25 mg./l. (as $CaCO_3$), falling again to 12·5 mg./l. by March 1952 as the result of heavy winter rains. Owing to the generally low rate of replacement in Loch Kinardochy (Brook and Woodward, 1956), the level of alkalinity in 1952 remained below that of 1951, rising only to 17 mg./l. in November. The level in 1953 was approximately the same as in 1951. The lower level in 1952 was in no way connected with the fertilization, and did not itself appear to influence the development of the algal flora which followed fertilization.

Calcium No analyses were made in 1951. The concentration immediately prior to fertilization was 23·5 mg. $CaCO_3$/l. After the addition of superphosphate the concentration rose to 26·1 mg./l., the increase being accounted for by the quantity of calcium dissolved from the superphosphate. A subsequent slow rise in calcium concentration was directly associated with the corresponding rise in bicarbonate alkalinity.

Nitrate The concentration of nitrate normally recorded during the spring and summer falls below 0·10 mg. N/l. This low level is maintained until the autumn, when a slow rise begins, and the concentration may exceed 0·25 mg. N/l. during the winter. Although concentrations recorded shortly after fertilization in 1952 were somewhat lower than those for the corresponding period in 1951, there is insufficient evidence to relate these lower figures to the development of the algal flora.

Ammonia The concentration of free ammonia nitrogen found in Loch Kinardochy, and in many other lochs in the area, is normally below 0·25 mg. N/l. Occasionally, and particularly in the autumn, much higher concentrations occur for short periods. After the application of fertilizer in 1952, the free ammonia concentration fell below 0·10 mg. N/l. within three weeks, the minimum of 0·05 mg./l. coinciding with a phytoplankton maximum. This outburst of phytoplankton ceased shortly afterwards, and during September and October the population of phytoplankton fell to the pre-fertilization level. In this period, abnormally high concentrations of ammonia were recorded, but as similar concentrations were recorded in other lochs at the same time, the rise cannot be attributed to the disappearance of the earlier phytoplankton outburst. During 1952 and 1953, however, there appeared to be some correlation between the largest phytoplankton maxima and minimal ammonia concentrations.

Soluble silica The concentration of soluble silica was markedly influenced by the fertilization, as shown in Fig. 3, where the recorded concentrations for the period 1951-1956 are shown. The normal silica cycle, as observed regularly in several other small lochs in the area, exhibits a rapid decrease in concentration during April and May, reaching a minimum in June of approximately 0·3-0·4 mg. SiO_2/l. From July onwards a slow rise takes place, the concentration exceeding 2·0 mg./l. by September or early October. The maximum level reached during the winter varies from loch to loch, but is generally between 3·0 and 5·0 mg./l. Similar cycles are recorded by Pearsall (1930).

It will be seen that the pre-fertilization cycle in Loch Kinardochy for 1951 is abnormal in that the minimum concentration reached was 2·2 mg./l., this level extending throughout most of July and August. The preceding and succeeding winter maxima were not unusual. No silica analyses were made before August 1950, but the values obtained after that date were almost identical with those obtained in the corresponding period of 1951. Applications of derris extract to the loch in 1949 and 1950, in an attempt to destroy the pike population, may have had some effect on the flora, although no such effects appear to have been recorded in the literature.

In 1952, the silica concentration decreased during May and June, and appeared to be approaching a minimum in July, although the concentration was still above 1·0 mg./l. Almost immediately after the addition of the fertilizer in mid-July the concentration fell rapidly to below 0·5 mg./l., very low concentrations being recorded early in August. The concentration rose later to approximately 0·5 mg./l. and remained at this level until October. This concentration is considered to be limiting for the growth of the diatom *Asterionella formosa* (Pearsall, 1932; Chu, 1942; Lund, 1950). The diatom in question was the dominant organism in the phytoplankton population during the first post-fertilization outburst, its numbers being highest on the 31st day after fertilization. By the 45th day it had almost disappeared, but

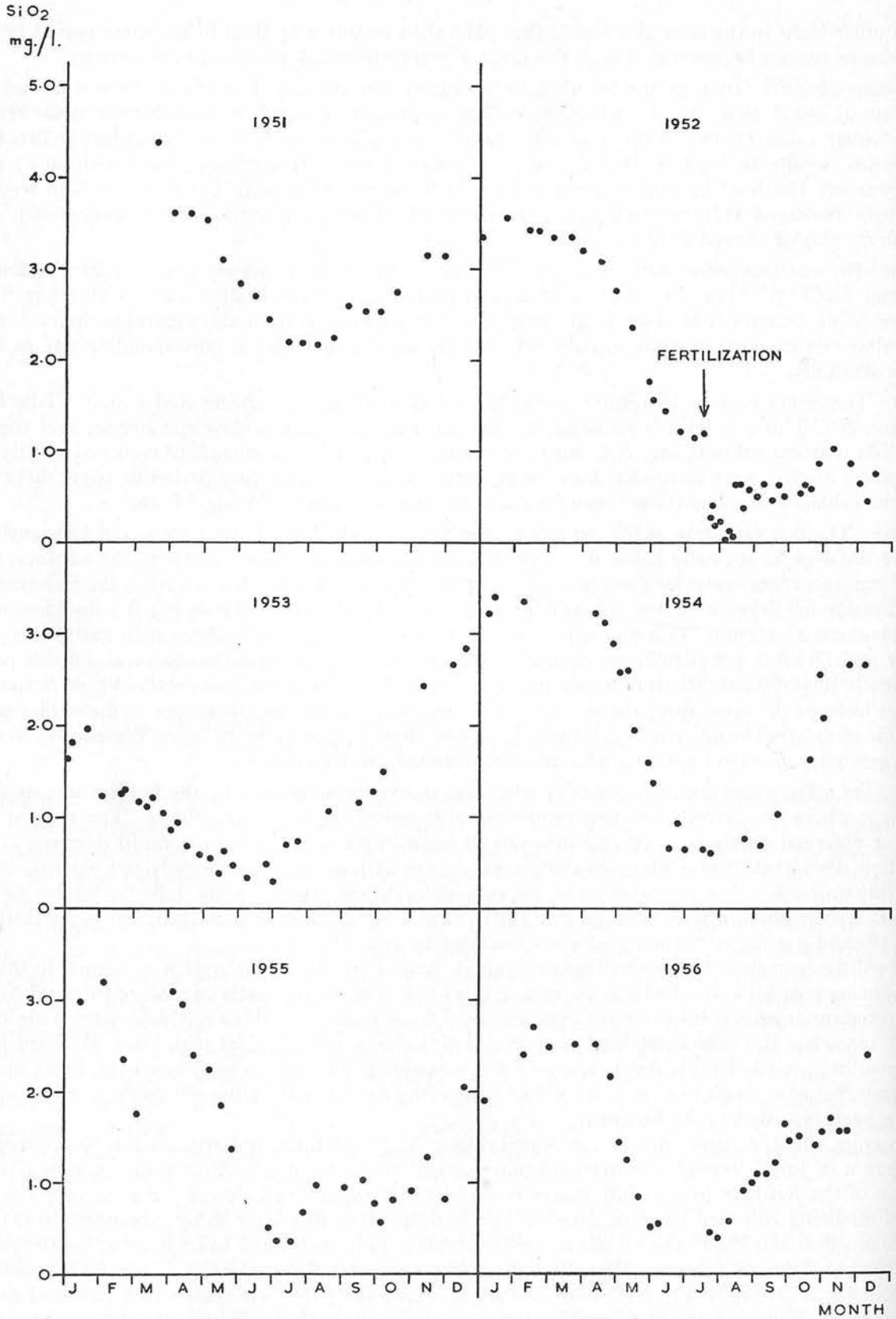


Fig. 3. Silica cycle for 1951-1956.

the silica concentration remained low until the 98th day. Soon after this, at the end of October, a period of rain occurred, and may have been responsible for the rise in silica concentration to 1·0 mg./l. By then *Asterionella* had been replaced by the diatom *Synedra acus.* var. *radians* as the dominant species, and a maximum of the latter occurred early in December, at which time the silica concentration again fell to 0·5 mg./l.

In the winter of 1952-53, the maximum silica concentration, 1·95 mg./l., was unusually low, and before the end of January a decline began, reaching a minimum concentration in June of 0·30 mg./l. This level was maintained until later in July, after which a slow increase continued throughout the remainder of the year, the concentration during the autumn being lower than normal.

The following winter, 1953-54, was not an abnormal one with respect to the silica cycle. The maximum of 3·39 mg./l. was reached in January, and the concentration remained high until mid-April, followed by the usual rapid seasonal decrease to a minimum in June. The 1954 cycle bore a close resemblance to the normal cycle, although the rise to the winter maximum was again slow. In 1955, the cycle was similar to that of 1954, but there was an even slower return to the higher winter concentrations. The winter maximum of 2·70 mg./l. was lower than those of the previous two winters.

In 1956, the cycle again appeared to be normal, the summer minimum being once more about 0·5 mg./l. in June and July. The autumnal rise was somewhat retarded in October and November, but by December the concentrations appeared to be increasing towards a normal winter maximum level.

Two points emerge from the analyses of the silica concentrations over the six-year period. The first is that, although a rather lower summer minimum concentration than usual had been reached by the time that the fertilizer was added, the three pre-fertilization minima recorded were abnormally high in comparison with other lochs in the area. The effect of the fertilizer addition was to cause the concentration to fall, in a matter of days, to an unusually low value, and it later rose to a summer level of about 0·5 mg./l. Moreover, the summer values for the following four years have always fallen to about this same level. The very large populations of diatoms produced as an immediate result of fertilization continued throughout the following winter, causing, apparently, a depression of the normal winter maximum of silica. The large phytoplankton population has progressively decreased since the spring of 1953, and, except for the brief large maximum of *Cyclotella glomerata* in May 1956, no further abnormally large numbers of diatoms have been recorded. However, in all years subsequent to 1952, the summer minima of silica have been lower than before fertilization. This seems to indicate that in a small body of water, such as Loch Kinardochy, where the ratio of macrophytes and attached algae to phytoplankton is high, planktonic diatoms are not primarily responsible for the spring decline in the silica concentration. It seems probable that a greater utilization of silica by the increased macrophytic and attached algal flora has probably been the most potent factor in maintaining this lower summer concentration.

FACTORS RESPONSIBLE FOR THE REMOVAL OF PHOSPHATE

In view of the undoubted complexity of factors concerned in reducing the phosphate concentration, it is difficult to suggest a simple explanation for the exponential nature of the decline. Among the factors which could be expected to take part in the removal of phosphate from the water are dilution, assimilation by macrophytes, planktonic algae, attached algae, bacteria and fungi, and adsorption to the bottom deposit. These factors will be discussed individually.

(*a*) Loss by dilution

It is known that the water flowing into the loch contains no detectable phosphate and as the results presented earlier in this paper (Tables 1 and 2) indicate that the water is thoroughly mixed, some loss of phosphate could occur by dilution.

In relation to the total volume of water in the loch, the quantity of water flowing through the loch daily is very small, particularly during the period under discussion. A simple formula expresses such a case of dilution, viz.

$$\ln\left(\frac{C}{C_0}\right) = -\frac{v}{V}(t-t_0)$$

where C=concentration of nutrient at time t
C_0 =concentration of nutrient at time t_0
v =total rate of inflow
V =total volume of loch

If the dilution process is considered as the sole factor responsible for the phosphate decline, the value of v can be calculated by employing the formula above. For the first 32 days, during which the decrease was faster than the overall average, the value of v is 5·48 cubic feet per second (155 litres/sec.), while the value for the full period of 105 days is 4·43 cubic feet per second (125 litres/sec.). The actual rate of flow which existed during the periods under consideration could not be measured, but from rainfall records it is estimated that the volume of water falling in the catchment area was equivalent to a rate of 1·64 cubic feet per second during the first 32 days (about 30% of the appropriate value calculated above), and 1·55 cubic feet per second for the 105-day period (about 35% of the value quoted above). Part of the volume of water falling in the area would be lost by evaporation or absorption by the dry ground surface, and the net average flows would undoubtedly be less than the figures calculated. The loss of phosphate attributable to dilution is probably between 15% and 25% of the total loss.

(*b*) Assimilation by macrophytes

The common species of macrophytes in Loch Kinardochy in 1952 were *Myriophyllum spicatum*, *Potamogeton praelongus*, *Lobelia dortmanna* and *Littorella uniflora*, with occasional specimens of *Potamogeton gramineus*. There were, in addition, two beds of *Carex rostrata* and one of *Equisetum fluviatile*, none of these being very extensive. Analysis of these species for phosphorus uptake following applications of fertilizer in other Scottish lochs have indicated no significant uptake by *Lobelia*, *Littorella*, *Equisetum* or *Carex*, but considerable uptake in the cases of *Myriophyllum*, *Potamogeton praelongus* and *P. gramineus*. The increases are greater during the growing period.

No quantitative survey of the macrophytic vegetation of the loch has been made, and consequently an accurate assessment of the influence of this section of the flora upon the rate of removal of dissolved phosphate was not possible. However, a similar fertilization experiment carried out in September in another hill loch provided some information on the rate at which *Myriophyllum spicatum* and *Potamogeton praelongus* could assimilate added phosphate (before analysis these plants were washed to remove as many attached algae as possible). Within three weeks, the phosphorus content of whole plants of *Myriophyllum spicatum* had increased from 0·95 to 2·58 mg. P/g. of dry plant material. In the case of *Potamogeton praelongus*, the phosphorus content of the stems showed no significant change, but that of the leaves rose from 1·41 to 3·20 mg. P/g. of dry plant material in nine days. The area of Loch Kinardochy covered by 5-10 feet of water, between which depths the species is commonly found, has been estimated as 17·4 acres (7·0 ha.) and this area could contain some 760,000 plants, assuming them to be distributed at a density of one per square foot, which does not seem unreasonable. An average plant, 7·5 feet high, has a dry weight of the order of 15 g., and the estimated population of this average size would be capable of removing 20 kg. of phosphorus on the basis of the figures quoted above. In the first nine days after fertilization the loss from solution amounted to some 40 kg.

(*c*) Assimilation by phytoplankton

The development of the phytoplankton population, and the succession of different species of algae, is more fully described elsewhere in this report, but this section is concerned only with that phosphorus in the water mass which did not exist as soluble inorganic phosphate (or phosphate liberated in the analysis by the acid reagents used). Analyses for total phosphorus of water samples from which only the larger zooplankton organisms had been removed were made frequently, and the differences between the values so obtained, and those for inorganic phosphate phosphorus, were recorded as organic phosphorus. This latter fraction is regarded as that phosphorus assimilated by phytoplankton, the smaller zooplankton (passing a 50-mesh net), bacteria and fungi, and also that in soluble organic compounds

or organic particulate material. It is assumed that any increase in the organic phosphorus fraction can be mainly attributed to planktonic organisms.

The level of organic phosphorus in Loch Kinardochy immediately before fertilization was 14μg./l. and the mean values obtained on several occasions during the few months following fertilization never rose beyond 27 μg./l. This level was attained on 11th August, when the concentration of cells of *Asterionella formosa* had reached a maximal value, and on 20th October, when some decomposition of the macrophytes might have taken place. In all but three other instances, the recorded organic phosphorus concentration was below 20 μg./l. The decrease of inorganic phosphate in the loch thus cannot be attributed to a corresponding uptake by the developing phytoplankton population.

Undoubtedly the phytoplankton cells utilised some phosphorus in their development, but the quantity removed from solution would have been very small. Mackereth (1953) found that *Asterionella formosa* can take up phosphate phosphorus from lake water at a concentration of less than 1 μg./l., and can continue growth until there is only 0·06 μg. P per million cells. One microgram of phosphate phosphorus could thus support 16 million cells. In cells from natural populations, Mackereth found phosphorus contents averaging 0·4 μg. per million cells at the time of an *Asterionella* maximum.

In Loch Kinardochy, the first *Asterionella* maximum, about 11th August, numbered about one million cells per litre, which would contain about 0·4 μg. P/l. on the above basis. At this time the inorganic phosphate concentration was 127 μg. P/l. and the organic phosphorus 27 μg. P/l. Thus the phosphorus contained in the phytoplankton was likely to have been only a small fraction of the total organic phosphorus. Subsequent plankton maxima reached concentrations ranging from 2 to 3 million cells per litre, but no unusually high organic phosphorus concentrations were recorded. The phytoplankton population (exclusive of nannoplankton) cannot therefore be regarded as an important factor in the removal of soluble phosphate from the water.

(*d*) Assimilation by attached algae

Before the addition of superphosphate to Loch Kinardochy, there was no evidence of any appreciable attached algal flora. However, within three days of the fertilization small growths were recorded in shallow water, and within ten days considerable green filamentous growths of *Zygnema* and *Spirogyra* were observed on stones in depths of water up to five feet, and also attached to the flower stems of *Lobelia*. By the 42nd day (25th August) the attached algae were covering stands of *Carex*, *Equisetum*, and *Potamogeton praelongus*. This attached flora continued to develop, and by the 63rd day (15th September) the upper parts of *P. praelongus* and *Myriophyllum spicatum* were completely enveloped. This algal felt persisted until late in October, though on 27th October, five weeks after the macrophytes had shown signs of decay and when the water temperature had fallen below 5°C, it was clearly less extensive. By 24th November the loch was covered with a layer of ice one inch thick and further detailed observations were impracticable. No signs of extensive growths of attached algae were seen when the ice melted in the following spring and none developed subsequently.

The attached algae were found to have a high phosphorus content, though no quantitative assessment was possible. The quantity of algae attached to all macrophytes was not considerable until about the 40th day, and developed rapidly during the following three weeks. By the 40th day the inorganic phosphate concentration had fallen to about 97 μg. P/l. and 93 kg. of phosphorus had been removed from the water. From then until the 60th day a further 13 kg. were removed, the rate of removal decreasing steadily. Unless it is postulated that the first-formed cells of filamentous algae stored large quantities of phosphorus, which were subsequently distributed throughout the later growth of new cells (the removal of phosphate from the water by the latter being small), it is difficult to associate the early rapid decrease of soluble phosphate with the later rapid increase in attached algae.

(*e*) Assimilation by bacteria and fungi

No information on the utilisation of phosphorus by freshwater bacteria and fungi is available, but the mass of these organisms in unpolluted lake waters is probably low in comparison with phytoplankton. Hayes (1955) suggests that the uptake of radiophosphorus by mud may be partly due to the action of bacteria, but he appears to take no account of bottom-living algae. Although no precise data are given,

it is certain that the quantity of radiophosphorus removed per unit area by the mud surface or associated organisms in Hayes' experiment was extremely small in comparison with the amount of phosphorus per unit area applied to Loch Kinardochy.

(*f*) Adsorption to the bottom deposit

The removal of soluble phosphate from the water by mud deposits has been described by various workers. Einsele (1938) observed that oxidised muds contain large quantities of ferric phosphate in their surface layers. Mortimer (1941) in his studies on the exchange of dissolved substances in lakes, postulated a hypothesis of chemical exchange involving adsorption to ferric hydroxide, or an organic-ferric complex, in colloidal form. He described the chemical changes occurring in the surface layers when, as the result of the formation of a hypolimnion, the deeper water is depleted of oxygen, resulting in the reduction of ferric hydroxide to ferrous hydroxide. This results in the release of adsorbed ions, including phosphate ions. The reverse process of adsorption of phosphate occurs when oxidising conditions are restored at the mud surface, as the result of the autumnal overturn.

In the present case of Loch Kinardochy, no hypolimnion has been observed to exist at any time, and the mud surface is believed to be permanently in the oxidised state. Under such conditions, phosphate and other ions will be continually adsorbed to the surface layer until equilibrium between the adsorbed and free ions is reached. Hayes *et al* (1952), using radiophosphorus in an unstratified lake, found that the P^{32} content of the mud deposit increased over a period of some four weeks, although they considered that there was no reason to suppose that the mud was wholly or largely responsible for the exchange mechanism. However, an active exchange between the dissolved phosphorus and that in solids generally (including plants) was postulated, based on the fact that the P^{32} concentration in the water declined, initially in an exponential manner, until a small but definite fraction remained permanently in the water. This small fraction was considered to be in equilibrium with the remainder of the P^{32} contained in the solids, an active exchange between the two fractions being suggested. Turnover times of the phosphorus in the water and in the solids could then be calculated. The equilibrium level in the water was found to be about 10% of the original concentration.

In the present case, the final concentration of phosphate phosphorus in solution in the water was less than 0·3% of the original concentration, and was below the detectable limit. Moreover, the exponential nature of the decrease in dissolved phosphate was continuous over the whole period of the decline, within close limits. The turnover time calculated for the full period of the decline is 36·9 days. This value is of the same order as those calculated by Hayes *et al* (1952) for nine English lakes.

The part which the mud surfaces may play in removing phosphate from the water can be better appreciated if the following facts, derived from analyses of Loch Kinardochy mud, are considered. A sample of surface mud, representative of the greater part of the area of the bottom deposit in the loch, had a total phosphorus content of 109 mg. P per 100 g. dry mud (mg. %). Of this, 41·3 mg. % were acid-soluble after two hours' continuous agitation with 0·1 N hydrochloric acid at 20°C. Only 2·7 mg. % were extracted with 0·5 N neutral ammonium fluoride at 20°C (exchangeable phosphate at pH 7). The sample contained 17·0% of organic matter as estimated by the loss on ignition. The saturation capacity of the mud for adsorbing (or otherwise removing) phosphate from solution was of the order of 110 mg. %.

A volume of 100 ml. of wet mud yielded a dry weight of mud of 17·82 g. The capacity of 1 ml. of mud for adsorbing (or removing) phosphate is thus 196 μg., or, if 1 sq. cm. of mud surface is considered, the capacity would be approximately 20 μg. of phosphate phosphorus per millimetre of depth. As the first few millimetres of the mud surface contain appreciably more water than the lower layers, this value would be somewhat reduced at the mud surface. However, the upper two centimetres of mud would be capable of adsorbing 300-350 μg. of phosphate phosphorus per square centimetre of surface. The process of adsorption will become slower as the upper layers become saturated, and the rate will be largely determined by the rate of diffusion through these layers.

Considering now the application of superphosphate to Loch Kinardochy, 148 kg. of phosphorus were distributed over an area of $1{\cdot}69 \times 10^9$ sq. cm. This is equivalent to 88·7 μg. P per sq. cm. The amount actually available for adsorption would be somewhat lower than this, after losses at the out-

flow, and by removal due to plants, etc., are allowed for, but the mud surface would clearly be able to accept this quantity while still remaining relatively unsaturated.

If adsorption to the mud deposit is regarded as the primary cause of the disappearance of dissolved phosphate, there are further aspects of the process which must be considered. The exponential decline of the phosphate concentration can be expressed as a percentage decrease in concentration per unit of time, i.e. the concentration decreases by a constant fraction of its value in a given time. If the return of phosphate to solution from solids is regarded as negligible (as would appear to be true in the present case), the differential equation $\frac{dC}{dt} = -K.C$ (where a change dC in the concentration C occurs in time dt) can be used to express the exponential decrease. This, in an alternative form, becomes $\frac{dC}{C} \cdot \frac{1}{dt} = -K$ (constant), i.e. the percentage decrease per unit of time is constant. It should be emphasized that other processes than adsorption may cause an exponential decline in soluble phosphate, but in this section adsorption to the mud surface will be considered as the sole possibility.

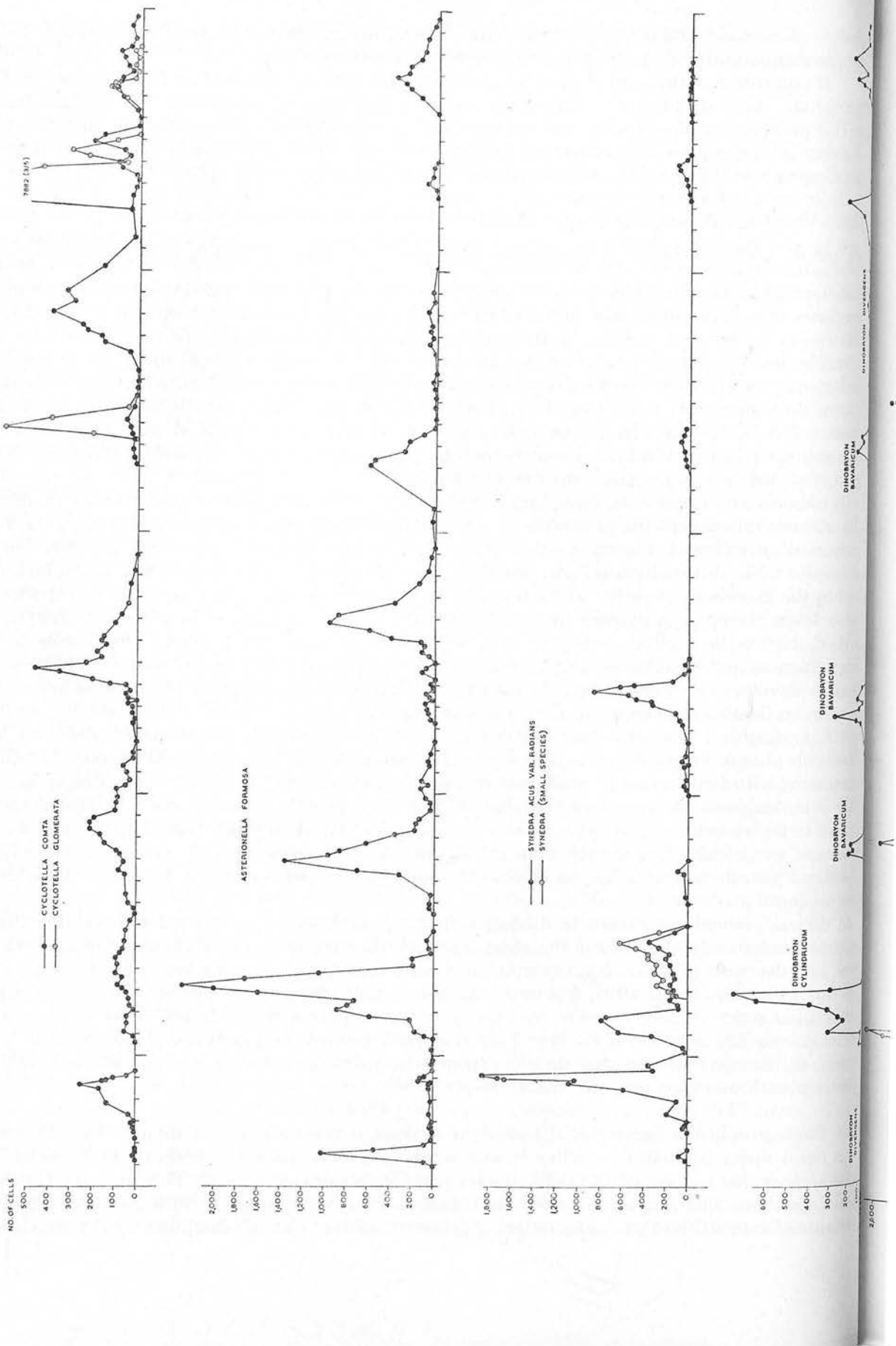
The loss of soluble phosphate from a column of water equal in height to the mean depth of the loch can be regarded as a gain by the mud surface at the base of this column. Hence the value of $K \times D$ where the constant K is in units of mg./litre per mg./litre per day and D is the mean depth in centimetres, can be expressed in μg./cm.^{2} per mg./litre per day. The calculated value of KD for the full 105-day period studied in Loch Kinardochy is 6·53 μg./cm.^{2} per mg./l. per day, and that for the initial 31-day period is 8·25 μg./cm.^{2}/ per mg./l. per day.

Laboratory experiments, using mud deposits from Loch Kinardochy under aerobic conditions in the absence of macrophytic growth or of any visible algal growth, have shown that the rate of uptake expressed in the above manner is only of the order of 1·6-2·3 μg./cm.^{2} per mg./l. per day. This range was valid when the total phosphorus adsorbed was 1-4 μg./cm.^{2}. When the phosphorus adsorbed at the end of the experimental period was 106 μg./cm.^{2}/, the rate of decrease was, as would be expected, somewhat lower, being 0·59 μg./cm.^{2} per mg./l. per day. In Loch Kinardochy, while the phosphorus adsorbed during the decline must have been somewhat less than 88·7 μg./cm.^{2}, the calculated rate of adsorption as quoted above is 6·53 μg./cm.^{2} per mg./l. per day. This rate is considerably greater than that achieved in any laboratory experiments, and implies that adsorption by the mud surface cannot have been the principal factor in the phosphate removal.

One further laboratory observation can be mentioned here. In two instances where the removal of soluble phosphate by mud adsorption was studied, the growth of benthic attached algae was deliberately encouraged. In both cases the phosphate decline was exponential, after a more rapid decrease initially due presumably to the uptake of phosphate by the algal growth. However, the exponential rate of decrease in both cases was greater (2·9 and 3·9 μg./cm.^{2} per mg./l. per day) than that which was obtained under otherwise identical conditions in the absence of algae (1·25 μg./cm.^{2} per mg./l. per day). Thus the algal growth undoubtedly was responsible for a more rapid removal of phosphate from the water in this particular case.

It was pointed out earlier, in dealing with the possible influence of algal growth, that the period of most extensive development of the algae occurred when the rate of removal of phosphate was already low, and decreasing further. It is nevertheless possible that this particular stage of development, observed on the macrophytic vegetation, followed a much earlier development of algae on the bottom deposits in the littoral zone. Algal growths were observed on stones in four to five feet of water within ten days of fertilization. The attached algal flora may thus have been developing during the complete period of the phosphate decline, and may therefore have been a significant factor in phosphate removal, in conjunction with adsorption to the mud surface.

Summarising the findings of the previous sections, it is suggested that dilution by inflowing water was not a major cause of the decline in soluble phosphate. Bacteria and fungi in the water and phytoplankton appear to have played only a minor part in phosphorus removal. The macrophytic vegetation was capable of removing a fraction of the dissolved phosphorus, together with attached benthic algae, the rate of removal by these agencies being greater than that due to adsorption by the bottom deposit.


NO. OF CELLS
CYCLOTELLA COMTA
CYCLOTELLA GLOMERATA
7882 (3/5)
ASTERIONELLA FORMOSA
SYNEDRA ACUS VAR. RADIANS
SYNEDRA (SMALL SPECIES)
DINOBRYON CYLINDRICUM
DINOBRYON BAVARICUM
DINOBRYON DIVERGENS

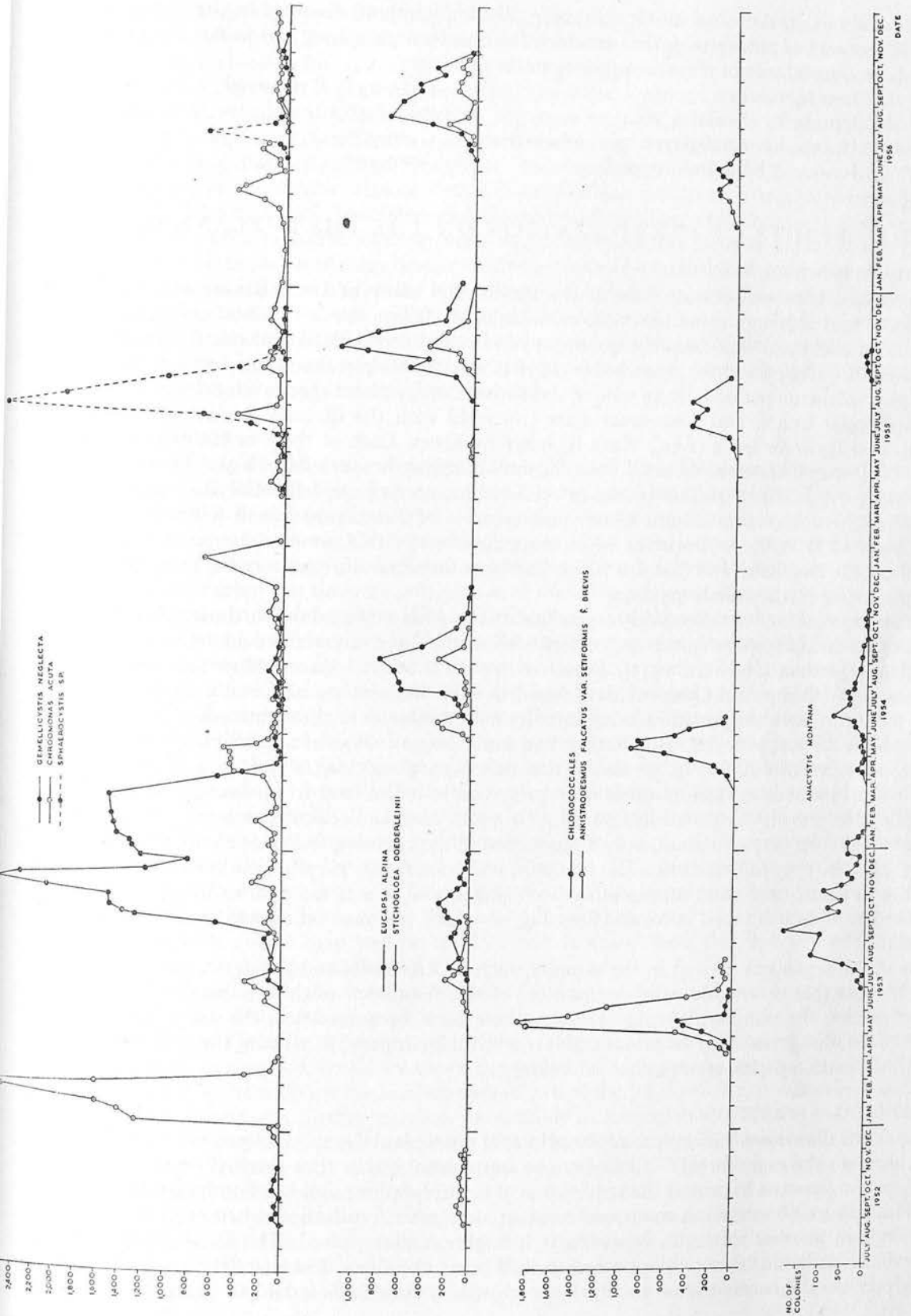


Fig. 4. Seasonal changes in the principal phytoplankton species, July, 1952, to December 1956.

The latter, while having the capacity for adsorbing all the phosphate dissolved in the water, is subject to a much slower rate of uptake than that at which the dissolved phosphate was in fact removed.

The relative importance of these four factors seems to be:

Loss by dilution	15-25% P removed
Uptake by plankton, etc.	> 1- 4% „ „
Uptake by macrophytes and attached algae	20-70% „ „
Removed by bottom deposit	10-30% „ „

THE EFFECTS OF FERTILIZATION ON THE PHYTOPLANKTON

(*a*) Introduction and Methods

The principal botanical observations in the fertilization study of Loch Kinardochy concern the phytoplankton, and although some observations were made before the addition of superphosphate, it was only after enrichment that frequent quantitative samples were analysed in detail. However, from samples collected during the three years before 1952 it was established that there was a fairly constant pattern of phytoplankton periodicity. In winter and spring the dominant species were *Dinobryon bavaricum* Imhof., *D. divergens* Imhof. and *Chroomonas acuta* Utermohl with the diatoms *Synedra acus* var. *radians* (Kg.) Hust. and *Cyclotella comta* (Ehr.) Kütz in lesser numbers. Each of these organisms, and a small population of *Asterionella formosa*, attained their maxima in spring between March and May, after which time their place was taken by several species of coccoid blue green algae (e.g. *Anacystis montana* (Lightf.) Drouet & Daily, *Gomphosphaeria lacustris* Chod. and colonies of *Botryococcus braunii* Kütz. and *Stichogloea doederleinii* (Schmidle) Wille. In autumn, while most members of this summer community persisted in small numbers, the flagellates and diatoms which had been dominant in winter and spring again became frequent, producing further small maxima.

From an examination of collections of plankton taken with a 180-mesh net during 1949 and 1950 a measure of the loch's trophic status before fertilization has been determined in terms of Nygaard's Phytoplankton Quotient (Nygaard 1949). From six net hauls taken between May and September determinations of the Compound Quotient were found to vary between 2·0 and 2·2, a figure which indicates that the loch may be regarded as being initially mesotrophic or slightly eutrophic.

Throughout the first year following fertilization samples were taken at approximately 0·5 m. below the surface from five sites A-E (Fig. 1) and in addition from 3 and 8 m. depth respectively from sites B and C. 10 ml. portions of these samples were preserved in iodine and from these aliquots, counts of the phytoplankton present were made using 1 ml. or 0·5 ml. Naumann cells, depending on the abundance of the plankton. When very abundant, only a proportion of the counting cell was examined. The analysis of samples taken in 1953 indicated that the plankton was remarkably evenly distributed throughout the loch, so that in subsequent years all sampling from sites B and C was discontinued and in their place one 0·5 metre sample was taken at a raft (R in Fig. 1) which was moored approximately in the centre of the loch.

Many of the organisms present in the samples, such as *Asterionella* and *Dinobryon*, are colonial algae and thus in order that reasonably valid comparisons of the abundance of these forms can be made with unicellular species, the numbers of cells in each colony have been recorded. An exception was made in the case of the blue green *Anacystis montana*, as it was virtually impossible to count the very large number of cells which make up this alga's spherical colonies.

(*b*) The initial effects

Fig. 4 shows the seasonal variations of the principal phytoplankton species from the time of addition of the fertilizer to the end of 1956. It can be seen from these graphs that the first significant increase became apparent fourteen days after the application of superphosphate and was dominated by *Asterionella formosa*. This species became most numerous some 31 days after fertilization when 1030 cells/ml. were recorded. Within another fortnight, however, it had almost disappeared. The short duration of this outburst which, it should be noted, appeared to start when the silica content of the water (see Fig. 3) was already below the concentration at which the growth of *Asterionella* is said to be inhibited (i.e. less

than 0·5 mg./l., Pearsall, 1932; Chu, 1942; Lund, 1950) may have been caused by the uptake of this nutrient, not only by planktonic diatoms but also by bottom living and attached forms. The latter in particular were observed to increase abundantly during this period. Only when the silica concentration in the loch increased above 0·5 mg./l., however, was there a second increase in planktonic diatoms. In this increase *Synedra acus* var. *radians*, which began to multiply in mid-October, replaced *Asterionella* as the dominant organism. The former continued to increase throughout November, a maximum of 1860 cells/ml. being attained on 2nd December. Accompanying the *Synedra* was a small, though well defined, outburst of the centric diatom *Cyclotella comta* which produced a maximum of 250 cells/ml. towards the end of November. Associated with this second flourishing of diatoms was a further depletion of silica and for a brief period its concentration again fell below the limiting value. Under normal circumstances the concentration of silica tends to increase considerably at this period of the year (see Fig. 3). It is of interest to note that even after the loch became ice covered on 27th November, *Synedra* continued to multiply, and between this date and the attainment of its maximum in early December, the diatom population almost doubled itself beneath the ice. For the remainder of the period during which the loch was ice covered, however, *Synedra* showed a steady decrease in numbers and for most of January 1953 an average density of 25 cells/ml. was recorded.

(*c*) LATER EFFECTS

1953—the spring plankton Before the disappearance of the ice both *Dinobryon cylindricum* Imhof. and *D. crenulatum* W. & G. S. West (Brook, 1954, p. 210 and Fig. 1, 7), and more especially *Chroomonas acuta* (Brook, 1954, p. 211 and Fig. 2, 1) began to increase. In January, ice and packed snow on the loch was one foot thick and a sample taken through this at sampling site C on 12th January was found to contain 2250 *Chroomonas* individuals per ml. The loch became ice free for a brief period between 23rd January and 4th February and during this time the populations of the three principal diatom species which were each to become dominant in turn, began to increase. However, when the ice cover re-formed there appeared to be a marked check in the increase in the numbers of these species. In contrast, *Chroomonas* continued to multiply vigorously and when the loch became ice-free once more it had attained its greatest abundance of 3,500 cells/ml. Then, within the following month it declined rapidly and became sporadic in its appearance for the remainder of the year with much smaller maxima in July and November. A similar though smaller production of flagellates and other phytoplankton organisms beneath ice had been recorded by Rodhe (1955) from lakes in Swedish Lapland which are covered with ice one metre or more in thickness for about eight months of the year, almost total darkness prevailing beneath. *Chroomonas acuta* has been present in nearly all samples from Loch Kinardochy since this first winter following fertilization, but as can be seen from the appropriate graph in Fig. 4, no maxima of comparable size to that which occurred beneath the ice have been observed. The largest maximum subsequently (700 cells/ml.) also occurred beneath ice, in January 1955. However, since somewhat smaller maxima (350-450 cells/ml.) have been found between May and July in each year, when predation by zooplankton on this small phytoflagellate may well be considerable, it would seem that low temperatures and light intensities are not the only prerequisites for its growth.

During the break in the ice cover at the end of January *Synedra acus* var. *radians* and *Dinobryon cylindricum* developed rapidly, attaining population densities of 650 and 300 cells/ml. within two weeks, while *Asterionella* and *Cyclotella* responded more slowly and increased to 150 and 50 cells/ml. respectively. As already stated, during the second ice cover the growth of all three diatom species, and of *Dinobryon*, appeared to suffer a check. With the final disappearance of the ice, however, it was only *Asterionella* and *Dinobryon* which showed any further increase, presumably at the expense of *Synedra* and *Cyclotella*, for no well defined maxima of these species occurred. The *Asterionella* maximum (2500 cells/ml.) occurred in early April, slightly preceded by that of *Dinobryon* (750 cells/ml.). This *Asterionella* maximum was thus of comparable magnitude to those of lakes showing a considerable degree of eutrophy.

Chemical analyses made during this period of spring diatom growth indicated that when the population, first of *Synedra* and later of *Asterionella*, began to decline, silica was still present in concentrations greater than 0·5 mg./l. and did not fall below this supposedly limiting concentration until early May. Phosphate, however, was barely detectable throughout the period and it can only be assumed that all

the organisms showing these exceptional increases in abundance were relying on reserves of this nutrient accumulated in their cells in excess of their immediate needs before these maxima developed (Lund, 1950). When the silica concentration had fallen below 0·5 mg./l., a condition which lasted from May to early July, a third increase in *Synedra* occurred, resulting in a maximum of 600 cells/ml. in early July. Two distinct size groups of cells were present in this population, the main portion being typical of the variety *radians* with cells of 100 μ or more in length. The remainder, which have also been plotted above the commoner form in Fig. 4, were only half this size. It is believed that the latter may have been largely derived from the abundant epiphytic population which showed considerable increases in abundance during this period. Indeed, the status of *Synedra acus* as a planktont would seem to be much more complex than that of other species owing to its epiphytic tendencies.

1953—the summer plankton The summer plankton in the first year following fertilization was dominated by a very large maximum of *Ankistrodesmus falcatus* var. *setiformis* f. *brevis* Nygaard, with lesser numbers of other Chlorococcales. Desmids of the genus *Staurastrum* also became relatively abundant in June and July when 32 per ml. were present for a time. Of these the most frequent were *S. cingulum* var. *obesum* G. M. Smith and *S. pingue* Teiling. In addition there was a considerable population of the colonial *Stichogloea doederleinii* which produced a maximum of 200 cells/ml. in July. *Ankistrodesmus falcatus* var. *setiformis* has shown no very significant development in subsequent years though there have been well defined, but successively smaller maxima of other species of Chlorococcales.

1953—the autumn plankton A considerable population of Cyanophyceae began to develop in August 1953 in which the colonial species, *Anacystis montana*, predominated and had its maximum of 180 colonies/ml. in mid-September. At the same time there was an autumnal maximum of *Asterionella* (1400 cells/ml.) which greatly exceeded those normally found in eutrophic lakes.

1953/54—the winter plankton Following this autumnal plankton there was an exceptionally abundant and unusual winter plankton dominated from mid-October 1953 until early April 1954 by the colonial isokont, *Gemellicystis neglecta* Teiling, in company with colonies of the slowly declining *Anacystis* population. *Gemellicystis* developed two maxima during the period, the larger in November with 2,600 cells/ml. and a smaller one in February of 1,500 cells/ml. The numbers of *Gemellicystis* declined rapidly throughout March and its final disappearance was associated with a considerable infection of the cells by the fungal parasite, *Rhizophydium fulgens* Canter.

1954—the spring plankton There was no spring maximum of *Asterionella* in 1954 as there had been in the previous year, and it seems possible that this diatom failed to increase significantly owing to the presence of, and consequent competition for nutrients by, the unusually large phytoplankton population of the preceding winter months. Only the diatoms *Synedra acus* var. *radians* and *Cyclotella comta* produced maxima of any size, and these occurred comparatively late in the season, in May and June respectively. Both were of about 850 cells/ml. and were preceded in April by a small maximum of *Dinobryon bavaricum*. It seems reasonable to infer that these unusually large *Synedra* and *Cyclotella* maxima, which it should be noted developed some considerable time after the disappearance of the large *Gemellicystis* population, arose by virtue of the absence of competition from *Asterionella*. In addition, the loch water at this period may have been enriched to some extent by decaying *Gemellicystis* cells.

1954—the summer plankton Chlorococcales and desmids were much less abundant in the summer of 1954 than in the previous year, though there was a slightly larger maximum of *Stichogloea* (290 cells/ml.). Of particular interest in the plankton during this period, however, were large colonies of the blue green alga, *Anacystis montana*. These attained a size of up to 15 mm. in diameter, and though only a few colonies of such dimensions have been found in the plankton, considerable numbers of smaller colonies, mostly between 0·5 and 3 mm. in diameter, have been observed in quantitative zooplankton samples, especially after storms. For example, 33 per litre were present in zooplankton samples collected on the 23rd June 1954.

Most of the colonies on reaching about 2 mm. in diameter tend to sink to the bottom of the loch where it seems they continue to enlarge. The floor of the loch became covered with these blue green, jelly-like spheres early in the winter of 1953 and bottom samples, taken with a Jenkin mud sampler

in the summer of 1954, indicated a density of about 2 large colonies (greater than 2 mm. diameter) per sq. cm. It appears that wind and wave action rolled these gelatinous spheres shorewards with the result that during the summer of 1954 many leeward bays of the loch became covered with a carpet of these algae which in places was a foot in depth. In the absence of any marked development of *Anacystis* in the plankton in subsequent years there has been no further recruitment to this bottom cover though the initial carpet still persisted throughout much of 1955 in the form of a tightly packed layer. This eventually decayed but apparently with no adverse effect on the bottom fauna in these localities.

Late in 1954 it was noted that there had been a very considerable increase in the abundance of the green colonial vorticellid *Ophridium ectatum* Mast, both on the stems of submerged macrophytes and on the bottom of the loch, usually at depths below 3 feet. Normally the colonies of this organism, which was fairly frequent in the loch before fertilization and which is of quite widespread occurence in Scottish freshwaters, do not exceed 20 mm. in diameter. However, at this time, and throughout 1955 and 1956, many colonies of more than five times this diameter were observed. Moreover, until 1955 none had been found on glass slides which were suspended in the loch in connection with studies of the attached algal flora. During that year, however, as many as 22, ranging in diameter from 2 to 15 mm. were found on a single 3×1 inch slide.

1954/55—the autumn and winter plankton The coccoid blue green *Eucapsa alpina* Clements and Shantz and *Asterionella formosa* dominated the plankton during this period and had maxima of 750 and 960 cells/ml. respectively. On their decline only a few phytoplankton organisms remained in the plankton, and in contrast to the abundant plankton of the two previous winters, the winter population of 1954-55 numbered less than 50 cells/ml.

1955 and 1956 During 1955 and 1956 there seems to have been a return to a more regular pattern of phytoplankton periodicity than during the first two years following enrichment, and at the same time there has been a general decline in the size of the maxima of those species which appeared to respond most to the addition of superphosphate. In contrast, *Eucapsa alpina*, *Stichogloea doederleinii* and to some extent *Cyclotella comta*, the numbers of which were comparatively low in the first two years following fertilization, have become re-established in the plankton.

In 1955, a sudden, though short-lived, increase in numbers of the small colonial diatom *Cyclotella glomerata* Bachm. occurred in late April, giving rise to a maximum of 600 cells per ml. in May. A much greater population developed in April 1956 which attained a maximum density of 7900 cells/ml. in early May. Similar, short-lived maxima of a *Sphaerocystis*-like species were present at the end of June 1955 when over 200 cells/ml. were counted and again in July 1956 when 700 cells/ml. were present.

(*d*) *Dinobryon* and fertilization

With reference to the 1953 spring maximum of *Dinobryon cylindricum* which occurred shortly before that of *Asterionella*, it should be noted that the former species had declined to 50 cells/ml. by the time the *Asterionella* population had reached a maximum. Little seems to be known about the periodicity of *Dinobryon cylindricum* but in those bodies of freshwater in which the closely related *D. divergens* has been found to occur, the latter's maximum abundance is usually attained after the spring diatom maximum. Records of this can be found for the English Lakes (Pearsall, 1932), several European lakes (Vetter, 1937; Dimitz, 1938) and for lakes in the United States (Hutchinson, 1944). Pearsall (*loc cit.*) suggests that low silica content and high N/P ratios are the factors controlling this periodicity, but Rodhe (1948) has found *Dinobryon* to be limited by high phosphate concentrations (between 100 and 200 μg. P/l.) and suggests that its maximum occurrence after the spring diatom outburst can be correlated with the utilization of phosphorus by the diatom population and its consequent fall to concentrations below the value which seems to inhibit the growth of this organism. Even at the time of the first *Dinobryon cylindricum* maximum in Loch Kinardochy phosphate, however, was barely detectable. The progressively smaller autumn and spring maxima which have followed this large population have been dominated by *D. bavaricum* or sometimes by *D. divergens* and it seems worth recording that all of these have occurred at higher nutrient levels than the diatom maxima with which they have been associated; that is before diatoms in the spring and after them in the autumn when nutrients have been increasing. Also worthy of note is the fact that

a small maximum of *D. divergens* was recorded soon after the phosphate fertilizer was added, in August, 1952, when the phosphate concentration was still between 260 and 300 μg./l.

It should be clear from the above account that, despite the rapid disappearance of the phosphate added in 1952, many phytoplankton species belonging to diverse algal groups showed striking outbursts of growth, especially during the first 18 months following the loch's artificial enrichment. Since that time, however, the size of these populations has for the most part shown a progressive decline, a fact clearly indicated by Table 3 in which the main maxima of the most abundant species are listed for each year since fertilization.

TABLE 3

Maxima and Period of Occurrence of Principal Phytoplankton Species since Fertilization, July, 1952 to December, 1956

	1952	1953		1954		1955		1956	
Asterionella formosa ..	1000 (Aug.)	2300 (Apr.)	1360 (Sept.)	No Max.	960 (Aug.)	600 (Apr.)	No Max.	100 (May)	300 (Sept.)
Synedra acus. var. radians	1860 (Dec.)	800 (Feb.)	No Max.	850 (May)	No Max.	100 (May)	No Max.	120 (May)	No Max.
Dinobryon spp.	55[1] (Aug.)	740[2] (Mar.)	200[3] (Oct.)	280[3] (Apr.)	No Max.	150[3] (Apr.)	60[1] (Nov.)	220[1] (Apr.)	290[1] (Oct.)
Chroomonus acuta ..	—	3500 (Feb.)	—	500 (May)	—	640 (Jan.)	400 (July)	420 (May)	—
Gemellicystis neglecta ..	—	—	2600 (Nov.)	1500 (Feb.)	—	—	104 (Oct.)	—	—
Chlorococcales[4]	—	2000 (May)		905 (May)		400 (July-Aug.)		180 (June)	
Staurastrum spp.	—	32 (June)		4 (June)		—		—	
Anacystis montana[5] ..	—	—	185 (Sept.)	—	75 (July)	—	10 (Oct.)	—	12 (Sept.)
Cyclotella comta	250 (Nov.)	—	210 (Nov.)	850 (June)		—	395 (Nov.)	102 (Apr.)	—
Stichogloca doederleinii ..	90 (Sept.)	—	200 (July)	290 (June)	275 (Sept.)	—	380 (Oct.)	240 (July)	165 (Sept.)
Eucapsa alpina	No Max.	—	260 (Oct.)	—	748 (Sept.)	—	1159 (Oct.)	—	763 (Aug.)
Cyclotella glomerata ..	—	—	—	—	—	500 (May)		7900 (May)	

1—*D. divergens*
2—*D. cylindricum*
3—*D. bavaricum*
4—includes *Ankistrodesmus, Dictyosphaerium* and *Planktosphaeria*
5—colonies per ml.

It is indeed unfortunate that no detailed quantitative study of the phytoplankton of Loch Kinardochy was made before fertilization. However, counts made subsequently from lochs of similar physical, chemical and biological characteristics suggest that the probable level of its standing crop varied annually between 10 and 500 organisms, and 20 and 1500 cells/ml. Fig. 5 shows the seasonal changes in the total numbers of phytoplankton organisms on a logarithmic scale from the time when fertilizer was added to December, 1956. From this figure it would seem that after two years of considerably increased plankton production this population had fallen to more normal levels by the third year. Table 4 gives the annual range of

TABLE 4

Standing Crop of Phytoplankton (organisms/litre) before and after Fertilization

Year	Range of Standing Crop	
	Minimum	*Maximum*
Pre-fertilization	10 (estimated)	500 (estimated)
1953	350	4000
1954	100	2000
1955	40	500
1956	40	500

the standing crop of phytoplankton before and after fertilization and it can be seen that in the first year after phosphate was added the maximum standing crop was eight times the estimated maximum before fertilization and four times the latter in the second year after fertilization. In 1955 and 1956 the standing crop, except during the brief periods of abundance of *Cyclotella glomerata* and *Sphaerocystis*, seemed to have returned to the estimated pre-fertilization level.

It is of interest to compare these figures with the maximum and minimum standing crops of phytoplankton from a series of other lochs representing a wide range of productivity which have been studied in some detail during the period of the present investigation. These standing crop figures are set out, with the pH and alkalinity ranges of the lochs concerned, in Table 5. This comparison suggests that the

TABLE 5

Trophic Status and Standing Crop of Phytoplankton of Loch Kinardochy and some other Scottish Lochs

Loch	Range of: pH	Alkalinity (p.p.m. $CaCO_3$)	Compound Phytoplankton Quotient[1]	Standing Crop of Phytoplankton (organisms/l.)	
				Minimum	*Maximum*
Loch Tummel	6·0–6·5	4–7	0·3	17	30
Loch Freuchie	7·0–7·3	10–14	0·5	—	576
Straloch	7·0–7·2	12–16	0·6	—	842
Loch Kinnaird	7·0–7·6	14–20	1·0	—	672
Loch Kinardochy	7·4–7·8	15–25	2·0	10	500 (pre fert.)
			2·0	40	4000 (post fert.)
Loch Dunmore	7·4–8·0	25–30	3·0	65	970
Loch Moraig	7·8–8·2	70–84	2·7	60	1800
Loch Leven	8·0–8·5	45–60	13·0	1020	7230

[1]See Nygaard (1949)

addition of superphosphate to Loch Kinardochy raised, at least for one year, the level of its phytoplankton production from a mesotrophic status to amounts characteristic of considerable eutrophy. There was, however, no corresponding increase of the compound phytoplankton quotient, which remained at a value of about 2·0.

OBSERVATIONS ON THE BOTTOM FAUNA

(*a*) The Littoral Zone

Quantitative sampling of the bottom fauna of the littoral zone was begun in August 1949, and continued regularly until the end of 1953. Intermittent samples were taken until March 1956. Sampling was carried out by means of trays as described by Moon (1935), except that wooden frames one foot square were used with bottoms covered either by hessian or 'Tygan' plastic screencloth. Some earlier samples were lost as the result of rotting of the hessian, but where this did not occur the results from the two types of tray did not differ significantly. Ice cover on the loch during winter was the major cause of

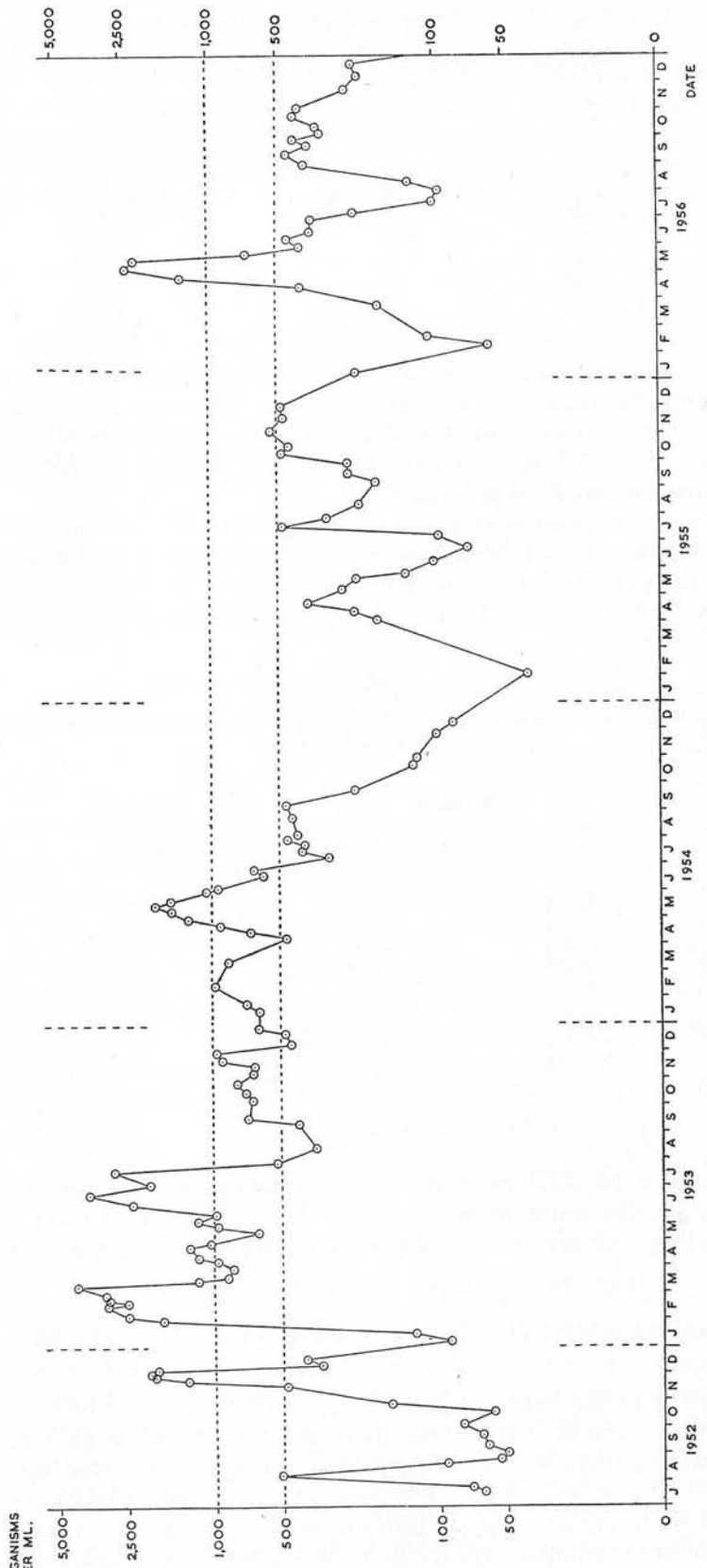


Fig. 5. Variations in the standing crop of phytoplankton, July, 1952, to December, 1956.

interruption in the continuity of sampling. The trays were set in pairs in about two feet of water at three sites, the positions of which are shown in Fig. 1 (sites I, II, and III).

The increase in the total number of organisms per tray after fertilization was mainly due to an increase in the population of *Gammarus lacustris*, although similar changes in the numbers of other organisms were also observed. It is thought that *Gammarus* was more accurately sampled by the method used than most of the other organisms present, and the results quoted in this section are therefore confined to changes in the numbers of this species.

The mean values of the numbers of *Gammarus* per square foot per site per month for each of the three

TABLE 6

Numbers of *Gammarus lacustris*/square foot in the Littoral Zone

	Site I	Site II	Site III
Pre-fertilization period (1949-1952)			
No. of samples ..	34	30	32
Range	5–70	5–56	1–79
Mean	34·0	21·7	24·0
Post-fertilisation period (1952-1953)			
No. of samples ..	17	17	17
Range	11-131	24-271	8–221
Mean	48·3	89·6	74·5
Post-fertilisation period (1954-56)			
No. of samples ..		9	
Range		60–256	
Mean		133·0	

sites are given in Table 6, for both the pre-fertilization and post-fertilization periods. The numbers of samples taken and the ranges of numbers per square foot are also shown.

The post-fertilization increase in the average number of *Gammarus* per square foot at sites II and III was statistically significant (at the 95% level), but the small increase at site I was not significant. A further series of seven samples at site II during 1954-56, with a range of 60-256 and a mean of 133 organisms per square foot, supported the impression that the *Gammarus* population at this site was more dense than in the pre-fertilization period. Sites II and III are situated on the lee shore of the loch, the prevailing wind being south westerly. Some time after fertilization it was observed that the amount of plant debris (see also p. 21) deposited along this shore had increased considerably. This accumulation of potential food material may have encouraged an aggregation of *Gammarus* and could thus account for the greater concentrations found, though there was no evidence of any corresponding decrease in the numbers of this organism at site I, or in the deeper water samples (see later).

On two occasions, in 1949 and 1950, attempts were made to eradicate pike from the loch by applying rotenone. Laboratory experiments have shown that *Gammarus* and other aquatic invertebrates are unharmed by far stronger concentrations of rotenone than were used in the field operations, and no effect was observed on the *Gammarus* of the loch during these operations. The last application of rotenone was made in May 1950, and the increase in *Gammarus* did not appear until the latter half of 1952. A reduction in the pike population in 1949 and 1950, if sufficient to reduce the predation on *Gammarus*, should have produced changes in the numbers of *Gammarus* well before the changes actually observed. These changes therefore seem more likely to be the result of fertilization, although the possibility that they reflect a natural fluctuation in the population cannot be ignored.

(*b*) The Sub-littoral Zone

The bottom fauna of the mud in the deeper water was sampled regularly from January 1952 until November 1953. Samples were taken at two monthly intervals from 5 sites which were identical with sites K1-K5 used for chemical sampling. The depths at these sites were 9, 14, 21, 28 and 20 feet respectively (2·7, 4·3, 6·4, 8·5 and 6·1 metres).

It was arbitrarily decided to take three samples per site on each visit and a subsequent experiment conducted at site K3 showed that three samples would be adequate to reveal any change of practical importance in the standing crop of bottom fauna in the deeper water sites (K3, K4 and K5), since the mean of the weights of bottom fauna from 3 samples should have a coefficient of variation of only 17%.

An Ekman grab was used for sampling the mud fauna since a preliminary experiment, comparing the results of samples taken with this and with a Petersen grab, revealed that the Ekman grab gave consistently higher numbers of animals per square foot and that the difference between the two methods was statistically significant.

The samples were screened through a 40 mesh sieve, the animals being picked out while alive and preserved in formalin-alcohol. Wet weights of the samples were determined by weighing them to the nearest 0·1 mg. in a dry weighing bottle after surplus external liquid had been removed with filter paper.

The samples at all sites were dominated by Chironominae, Tanypodinae, Sphaeriidae and *Gammarus lacustris*, and at the deeper water sites (K3, K4, and K5) very few other organisms occurred. At sites K1 and K2 other organisms such as Trichoptera, Hirudinea and Oligochaeta were more common, and the sporadic occurrence of such organisms led to marked and apparently erratic fluctuations in the wet weights of samples from these two sites.

The results from these shallower water sites (K1 and K2) have not been given here because of the fluctuations which occurred in them. The results from each of the other three sites (K3, K4 and K5) were much more consistent and since their values were very similar the results from these sites have been combined in preparing the averages given in Table 7. Three samples taken from site K3 during November 1955 gave averages of 315 animals and 0·549 g./sq. ft. From the table it will be seen that the

TABLE 7

Bottom Fauna in the Deeper Water of Loch Kinardochy (mean values per square foot from Sites K3, K4 and K5)

Month	Mean Numbers of Organisms			Mean Weight of Organisms (g.)		
	1952	1953	1955 (K3 only)	1952	1953	1955 (K3 only)
Jan. ..	146[1]	179		0·220[1]	0·383	
Mar. ..	125	141		0·307	0·383	
May ..	73	115		0·129	0·366	
July ..	71[2]	145		0·163	0·464	
Sept. ..	94	88		0·310	0·446	
Nov. ..	147	107	315[3]	0·343	0·322	0·549[3]

[1]—Mean of 6 samples; [2]—Mean of 8 samples; [3]—Mean of 3 samples; otherwise the figures quoted are the means of 9 samples

standing crop of bottom fauna was greater in 1953 than in 1952, but the differences were small, although the single estimate in 1955 suggests that the increase may have become greater in subsequent years. As was stated in the section on the littoral fauna, it is also possible that these differences are within the normal range of year-to-year fluctuations in the density of bottom fauna. No assessment of the latter is possible in the absence of a regular long-term programme of sampling before fertilization.

DISCUSSION

It is difficult to compare the results of the present investigation with those obtained by previous workers because there is so much variation, in lake fertilization experiments, in the type of fertilizer used, the frequency of its application and in the scope and period of the post-fertilization observations. Many earlier workers have used nitrogen-phosphorus-potassium mixtures either alone (e.g. King, 1943;

Ball, 1948; Smith, 1948; Langford, 1950; Ball and Tanner, 1951; Barrett, 1953; Weatherly and Nicholls, 1955) or with calcium (e.g. Taylor, 1944; Surber, 1948); Nelson and Edmondson (1955) used a nitrogen-phosphorus mixture, Wales (1946) an organic phosphorus fertilizer, though Einsele (1941) used superphosphate alone as a fertilizer. In most cases several applications of fertilizer were made though Smith (1948) and Langford (1950) have studied the effects of a single addition of fertilizer. Most of the previous investigators do not seem to have studied the effects of their treatments for more than two years afterwards. Barrett (1952), however, continued his observations for three years, Nelson and Edmondson (1955) for three to four years and Juday and Schloemer (1938) and Weatherly and Nicholls (1955) for five years. Where chemical analyses were made after treatment, most previous workers have confined their attention to phosphate in the water, but Barrett (1952) also studied the phosphorus in the mud and Weatherly and Nicholls (1955) studied the phosphorus in the water, the plankton, the macrophytes and the mud. Biological observations after fertilization have chiefly concerned the plankton and the fish, though Smith (1948) and Weatherly and Nicholls (1955) studied the bottom fauna as well.

Although there are, therefore, many differences between the conditions of the present study and those of previous investigations, the initial results seem basically similar, namely a rapid and considerable increase in the phytoplankton population, a considerable increase in the amounts of attached, principally filamentous algae soon after the phosphate was added, and a rapid removal of the phosphate from solution.

In Loch Kinardochy, although only a single application of superphosphate was made, a very marked increase in the standing crop of phytoplankton was maintained for some eighteen months after enrichment and it was only following the second summer after fertilization that this population seemed to return to more normal levels. Hayes *et al* (1952), however, doubt whether there is enough phosphorus left in the water to produce a stimulus to plankton growth in fertilization experiments even in the spring following enrichment. In Loch Kinardochy this stimulus was clearly maintained until the second spring following fertilization, when large numbers of *Gemellicystis neglecta* were present. This species had been abundant throughout the previous winter. During the summer of 1954 (almost two years after enrichment), however, the bottom of the loch became covered with large numbers of gelatinous spheres of the colonial blue green alga, *Anacystis montana*, which originated in the plankton.

The increase in the amount of attached algae did not seem to persist as long as that of the phytoplankton and no large amounts of these algae were observed in subsequent years. Their abundance may, however, have been reduced by the browsing of the increased bottom fauna population.

The disappearance of the added phosphate cannot, however, be attributed, to any appreciable extent, to the increase in the numbers of phytoplankton. Indeed, calculations based on the values found by Mackereth (1953) indicate that the phosphorus content of even the largest phytoplankton populations observed during the present experiment would account for only a minute proportion of the phosphate removed.

Some earlier investigators (e.g. Breest, 1921; Einsele, 1938; Mortimer, 1941; Orr, 1947; Hayes, 1951) have suggested that the removal of phosphate by a muddy bottom deposit plays an important part in causing the disappearance of this fertilizer. This possibility has been considered in some detail in the present investigation, but it does not seem to be a likely reason for the disappearance. In particular, laboratory experiments have shown that, whilst the mud in Loch Kinardochy might have the capacity to absorb all the phosphate added, in fact it disappeared much too quickly from the loch, for this process to have been the principal agent in its removal.

Hutchinson and Bowen (1950) suggested that macrophytes could be an important factor in causing the disappearance of phosphate in small lakes and this also seems to have been the case in Loch Kinardochy. During the course of the present investigation analyses were made of plants of *Potamogeton praelongus* and *Myriophyllum spicatum*, freed as far as possible from attached algae, to determine the rate at which they could assimilate added phosphate. The results indicate that a 2-2½ fold increase in the phosphorus content of the dried plants had taken place within 7-9 days. This result is comparable with that obtained by Weatherly and Nicholls (1955) who found that *Myriophyllum elatinoides* showed a similar increase in phosphorus content together with an increase in abundance following the addition of a nitrogen-phosphorus-potassium fertilizer to a lake in Tasmania. As previously mentioned, considerable growth of filamentous algae had developed on the macrophytes within 6 weeks of the fertilizer being

added to Loch Kinardochy and these might well have taken up significant amounts of phosphate. It has been estimated that the macrophytes and their epiphytes accounted for the largest fraction of the phosphate which disappeared from solution during the period following fertilization.

There is some evidence of a numerical increase in the bottom fauna following fertilization. The increase in the numbers of *Gammarus lacustris* in the littoral zone was statistically significant, and in this connection it is interesting to note that the most striking changes in the bottom fauna of Crecy Lake, New Brunswick, after fertilization were increases in the numbers of the amphipod, *Hyallela* (Smith, 1948). The numerical changes in the sub-littoral bottom fauna of Loch Kinardochy were, however, not significant statistically so that, in general, changes in the bottom fauna following fertilization were less definite than those in the phytoplankton.

It must be pointed out that the experiment described in the foregoing paper was the first of a series conducted in small lochs in various parts of Scotland. Although in this experiment the chemical and botanical aspects have been studied almost to the exclusion of the others, in the subsequent studies, the details of which will be published later, the emphasis has been largely on observing the influence of the addition of various types of phosphatic fertilizers on the growth of trout.

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SUMMARY

1. The paper presents some of the results of the fertilization with calcium superphosphate of a 41-acre (16·6-ha.) hill loch in north-west Perthshire, Scotland.

2. Regular determinations of pH, bicarbonate alkalinity, calcium, nitrate, ammonia, soluble silica and inorganic and organic phosphorus, were made for about 18 months before, and in most cases for 18 months, or longer, after fertilization.

3. Particular attention was paid to the removal of the added phosphate, and an attempt has been made to assess the importance of the various factors which could have been responsible for this removal. These include loss by dilution, assimilation by macrophytes, phytoplankton, attached algae or by bacteria and fungi, and removal by adsorption to the bottom deposits of the loch.

4. It is shown that of the above factors, assimilation by the submerged macrophytic vegetation and the attached algal flora of the loch were probably the most important in causing the disappearance of phosphate.

5. The quantitative changes in the phytoplankton of the loch following enrichment have been studied for four and a half years. In the first year after fertilization the standing crop of these organisms increased by about eight times. There was a decline to a crop of about half this level in the second year, while during the third and fourth years this population seems to have returned to more normal numbers.

6. Some observations have been made on the changes in the bottom fauna in both the littoral and deeper waters of the loch and the results suggest that there was a significant numerical increase in these animals, especially in the littoral zone, following fertilization.

7. The results of this experiment are briefly discussed in relation to the findings of other workers in this field of investigation.

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Changes in the phytoplankton of some Scottish hill lochs resulting from their artificial enrichment

A. J. Brook (Pitlochry, Scotland)

With 7 tables in the text

Chemical analyses having shown that phosphate is for the most part undetectable in the waters of many Scottish hill lochs, this important nutrient was added to a loch in N.W. Perthshire as part of a series of fertilization experiments. Loch Kinardochy, the loch so treated, whose maximum depth is 9.2 m and mean depth estimated as 2.7 m, lies in moorland country some 360 m above sea level. From analyses made in 1950 and 1951 the pH of its waters before fertilization was found to vary between 6.8 and 7.8, though most frequently it was nearly neutral, with alkalinities ranging usually between 15—25 ppm $CaCO_3$. Two tons (2032 kg) of calcium superphosphate were added on 14th July 1952 resulting in an initial increase in phosphate-phosphorus concentration of between 330 and 370 µg/l. The course of the decline of phosphate from this high level until it became undetectable was exponential and took about 105 days. Whilst observations and calculations concerning this removal of phosphate from the water indicated that uptake by macrophytes and attached and bottom living algae in the loch were probably the most significant factors, this artificial enrichment nevertheless had a profound effect on the phytoplankton, quantitative observations on which have now been carried out at fortnightly intervals or less for the past four years.

From samples collected before fertilization it was established that in winter and spring the dominant phytoplankton species were *Dinobryon bavaricum*, *D. divergens* and *Chroomonas acuta* with the diatoms *Synedra acus* var. *radians* and *Cyclotella comta* present in lesser numbers. Each of these organisms, and a small population of *Asterionella formosa*, attained their maxima between March and May, and were then replaced by species of coccoid blue green algae (*Anacystis montana*, *Gomphosphaeria lacustris*, etc.) and colonies of *Botryococcus braunii* and *Stichogloea doederleinii*. In autumn, while most members of this summer community persisted in small numbers, the flagellates and diatoms which had been dominant in winter and spring usually became frequent again, producing further small maxima.

From net hauls taken before fertilization the loch's original trophic status has been determined in terms of NYGAARD's Phytoplankton Quotient Hypothesis (NYGAARD 1949). From six samples collected between May and September

between the years 1949 and 1951 the Compound Quotient was found to vary between 2.0 and 2.2, a value indicative of a mesotrophic loch.

The response of the phytoplankton to the addition of superphosphate was rapid, a very significant increase in its abundance becoming apparent 14 days after enrichment when a maximum of more than 1000 cells per ml of *Asterionella formosa* developed. After this, many other species belonging to diverse groups (Diatomaceae, Cyanophyceae, Chrysophyceae, Chlorococcales and Isokontae) showed in turn striking and sometimes prolonged outbursts of growth, especially during the first 18 months. Since then, however, these populations have shown a progressive decline. This decline is indicated in Tables 1 and 2 in which the principal maxima of the most important species are listed for each year since fertilization. Table 1 relates to those species with well defined spring and autumn maxima and Table 2 to species with a less well defined periodicity.

Table 1. Maxima of phytoplankton species with spring and autumn maxima in Loch Kinardochy 1952—1956.

Species	1952	1953		1954		1955		1956
	autm.	spr.	autm.	spr.	autm.	spr.	autm.	spr.
Asterionella formosa . . .	1000	2300	1360	no max.	960	600	50	100
Synedra acus var. *radians*	1860	800	no max.	850	no max.	100	no max.	122
Dinobryon spp.	55[1]	740[2]	200[2]	280[3]	no max.	150[3]	60[1]	218[1]

[1] = *Dinobryon divergens*, [2] = *D. cylindricum*, [3] = *D. bavaricum*.

Table 2. Maxima of phytoplankton species with undefined periodicity, Loch Kinardochy 1953—1955.

Species	1953	1954	1955
Chroomonas acuta	3500 (Feb.)	500 (May)	640 (Jan.) 400 (July)
Gemellicystis neglecta	2600 (Nov.)	1500 (Feb.)	104 (Oct.)
Chlorococcales[1]	2000 (May)	905 (May)	400 (July—Aug.)
Anacystis montana[2]	185 (Sept.)	75 (July)	10 (Oct.)
Staurastrum spp.	32 (June)	—	—

[1] = includes *Ankistrodesmus falcatus* var. *setiformis*, *A. acicularis*, *Dictyosphaerium pulchellum* and *Planklosphaeria gelatinosa*.

[2] = colonies per ml.

Whilst the species in the above tables have shown a steady decline in abundance since 1952, there has been a reappearance of three autumnal species which

were quite numerous before fertilization but which showed little development in the autumnal plankton of 1952 or 1953. The progressive increase in the size of the maxima of these species is clearly indicated in Table 3.

Table 3. Phytoplankton species showing progressive increase in abundance since fertilization.

Species	1952 (post-fertilization)	1953	1954	1955
Cyclotella comta	250 (Nov.)	210 (Nov.)	850 (June)	395 (Nov.)
Stichogloea doederleinii	90 (Sept.)	200 (July)	290 (June) 275 (Sept.)	380 (Oct.)
Eucapsa alpina	no max.	260 (Oct.)	748 (Sept.)	1159 (Oct.)

It is unfortunate that no fully reliable estimates of phytoplankton density were made from Loch Kinardochy before fertilization. However, counts made subsequently from lochs of similar chemical and biological characteristics suggest that the standing crop probably varied annually between 10 and 500 organisms per ml. In Table 4 the annual variation in standing crop of phytoplankton in terms of organisms per ml before and for each year since fertilization are given. It can be seen from this that in the first year after fertilization the standing crop was increased above the normal by a factor of 8 and in the second by 4, while in the third year, numbers had returned to the prefertilization level.

Table 4. Annual range in abundance of Standing Crop of Phytoplankton before (estimated) and after fertilization.

Year	Range of Standing Crop (organisms per ml)	
	Minimum	Maximum
Pre-fertilization (estimated)	10	500
1953	350	4000
1954	100	2000
1955	40	500

These increases in abundance of the phytoplankton produced no significant changes in the trophic status of the loch as determined by NYGAARD's Compound Quotient which has remained in the region of 2 since fertilization.

A further series of fertilization experiments were initiated in 1954 in Sutherland (in the N.W. corner of Scotland), these being primarily designed to study the effects of the addition of various mineral nutrients on trout growth. Since the

treated lochs lie some 200 miles or more from the laboratory, it was not feasible to follow in detail, as was done for Loch Kinardochy, the quantitative changes produced by fertilization in the phytoplankton. However, occasional net hauls have been taken, the analyses of which have revealed much more radical changes in the specific composition of the plankton, as indicated by quotient determinations, than were produced in the earlier experiment and which thus are worthy of comment.

Six lochs were involved in these experiments, ranging in size from 6 to 20 acres (2.43 and to 8.09 hectares) two of which served as controls while the remainder were treated in the following way (Table 5).

Table 5. Enrichment of Sutherland Lochs 1954 and 1955.

	1954		1955			Pre-fertilization	
	June	Aug.	April	June	Aug.	pH	Alkalinity
L. an Smuraich . .	$Ca+NPK^2+NaNO_3$	$NPK+NaNO_3$	NPK	NPK	NPK	5.5—6.0	1—2
L. Grosvenor . . .	$Ca+SP^1$	—	SP	SP	SP		
L. Mhullaich . . .	Control	—	—	—	—	6.5—7.0	5—10
L. na Beiste Brice	$NPK+NaNO_3$	$NPK+NaNO_3$	NPK	NPK	NPK		
L. Daimh Beg . .	Control	—	—	—	—	7.0—7.5	10—20
L. Daimh Mor . .	SP	SP	SP	SP	SP		

[1] SP = Calcium superphosphate.
[2] NPK added in proportions 2.5 : 1 : 1 approximately.

The applications in 1955 were made with the intention of saturating the mud on the bottom of the treated lochs with phosphorus, the amounts added being calculated on the assumption that the adsorbing layer is between 1.5 and 2.0 cm deep (MORTIMER 1941) and that an application of 250—300 µg per cm^2 would saturate it. From the chemical standpoint particular attention was paid again to the fate of the added phosphate. Of special interest with reference to the plankton were those analyses made to determine the amount of this nutrient converted to organic form, soluble or particulate, in the water. In the two lochs treated with superphosphate, Loch Grosvenor and Loch Daimh Mor, amounts of up to 50 µg per l have been found, while the two NPK-treated lochs have for a time contained more than three times this amount. Untreated lochs in the area normally give values of 4—7 µg organic P/litre.

These marked increases in organic phosphorus concentrations were associated with a considerable development of the phytoplankton, especially in the NPK-treated lochs where pronounced blooms of Chlorococcales and Cyanophyceae developed. Moreover, their intense photosynthetic activity caused the pH of these two lochs to rise at times to values of 8 to 10 in contrast to their normal value of 6 to 7.

The Compound Phytoplankton Quotients of each loch were determined before treatment and, wherever possible, monthly after fertilization. It can be seen from the accompanying table (Table 6) that no significant change was apparent in the quotients following the 1954 enrichments, but when fertilization was continued in 1955 very striking increases, particularly in Loch na Beiste Brice, became apparent. On the basis of NYGAARD's criteria of trophic status in relation to the Compound Quotient, it is clear that the previously markedly oligotrophic Loch Smuraich and Loch Grosvenor became for a period distinctly eutrophic. The effect was even more pronounced in Loch na Beiste Brice which showed a considerable degree of eutrophication which persisted for a considerable time, though Loch Daimh Mor, which was enriched with superphosphate only, showed no significant change.

Table 6. Compound Phytoplankton Quotients of Enriched Sutherland Lochs 1954 and 1955.

Date	Smuraich (NPK)	Grosvenor (Ca + Super P)	Mhullaich (Control)	Beiste Brice (NPK)	Daimh Beg (Control)	Daimh Mor (Super P)
1954						
May	0.3	0.3	0.5	0.7	0.8	1.6
August	0.2	0.17	0.5	0.5	0.9	1.0
1955						
April	2.0	—	0.5	0.5	1.0	1.0
May	—	0.2	0.5	0.6	0.9	1.0
June	3.0	—	1.0	2.7	—	2.0
August	6.0	5.0	0.8	3.2	0.9	1.7
	—	—	—	6.0	—	—
September . . .	1.7	3.0	0.6	11.0	0.8	—

These results raise the question, how sensitive is the Plankton Quotient to sudden changes in nutrient status?

Fertilization experiments suggest that enrichment by itself does not necessarily bring about these changes for the Quotients were unaltered after the 1954 fertilizations, as was also the case in the earlier experiment in Loch Kinardochy.

It was only when considerable blooms developed that significant increases in the quotients became apparent. Since the maximum concentrations in the water of the added nutrients, which were all utilized very rapidly, were no greater in 1955 than in the previous year, it is suggested that it was the effect of the superabundance of algae themselves which was decisive. It has already been stated that in the two NPK-treated lochs, when blooms of Chlorococcales and Cyanophyceae developed, there were considerable fluctuations in pH which for a time varied from 8 to 10 instead of the normal 6 to 7. These increases and the general instability in hydrogen ion concentration were, it is believed, largely responsible for the disappearance of desmids from the plankton, the factor largely

responsible for the increase in the quotients. Added to this, however, the now well established phenomenon of the production of anti-biotic substances by freshwater algae must also be considered as possibly playing an important part in altering the specific composition, and hence in increasing the quotients in those enriched lochs where blooms developed. Of particular significance in this connection is the demonstration by LEFEVRE, JAKOB and NISBET (1952) of the antagonistic action of abundant growths of planktonic blue green algae on species of desmids. Thus it appears that phytoplankton quotients are not influenced by sudden radical changes in nutrient status produced by fertilization unless these changes trigger-off profound biological changes.

Table 7. Classification of English Lakes.

	Lake shore % rocky	Drainage % cultivable	Relative transparency of water	Water analysis ppm.			Compound Phytoplankton Quotient (May—Sept. 1955) Min. — Max.
				Lime	N	Organic matter	
Ennerdale . . .	66	5.4	8.3	2.4	.025	5.6	0.2 — 0.5
Buttermere . . .	50	6.0	8.0	2.8	.028	5.5	0.3 — 0.5
Crummock . . .	47	8.0	8.0	4.0	.035	6.6	0.2 — 0.3
Haweswater . .	25	7.7	5.8	4.0	—	4.3	0.9 — 1.6
Derwentwater .	33	10.0	5.5	7.5	.025	4.4	0.9 — 1.2
Bassenthwaite .	29	29.4	2.2	7.9	.053	6.1	0.4 — 0.8
Coniston	27	21.8	5.4	4.8	—	7.1	1.0 — 2.2
Ullswater	28	16.6	5.4	5.6	.047	11.4	2.0 — 3.5
Windermere . .	28	29.4	5.5	10.1	.103	10.8	0.6 — 0.9

With reference to more gradual increases in nutrient status additional support for the above thesis would seem to be provided by the phytoplankton quotients which have been determined for Windermere and Loch Leven, Kinross. It is well known that during the past century or more there has been considerable enrichment of Windermere through the influence of the greatly increased human habitation round its shores. Despite this, however, in terms of NYGAARD's Compound Quotient its phytoplankton is indicative of oligotrophic to mesotrophic status, determinations from samples collected between May and September varying between 0.6 and 0.9. Loch Leven has also been considerably enriched by agricultural and urban development over a similar period of time. Even fifty years ago, from the records of BACHMANN (1907), some ten species of desmids were present, the Quotient as determined from his analysis being $19/10 = 1.9$. Frequent and extensive sampling of this loch during the past four years have revealed that now only four species of desmids occur, the Quotient having increased to $29/4 = 7.2$. Loch Leven, however, at least in recent years, has produced very considerable blooms of blue green algae, up to 10,000 filaments per ml of *Oscillatoria bornetii* for example, having been recorded during the summer of 1937

(Rosenberg 1937) and 20,000 filaments of the much smaller *O. limnetica* were present in May 1954. In contrast, although Windermere supports an abundant plankton, no populations of the magnitude which could be said to constitute a true bloom have been found in the lake.

The anomalous quotient of Windermere is further emphasised in Table 7 in which nine of the English Lakes, including Windermere, have been arranged, on the basis of certain physical and chemical characters, in a series from primitive to evolved. The final column of the table shows each lake's plankton quotient as derived from samples collected between May and September 1955. It is clear that the considerably enriched Windermere is a misfit in this series. On the other hand, accepting the hypothesis of lake evolution, it is apparent from this table that when enrichment proceeds naturally, and presumably very slowly, the composition of the phytoplankton does change accordingly without the influence of blooms.

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Discussion

Nygaard: A phytoplankton index may be computed in different ways; the quantitative concept may be introduced or not. Instead of using the taxonomic groups of the Compound Index, it may possibly be an advantage to employ taxonomic units the ecology of which we know, or believe we know. Thus the *Melosira* species are not all of them eutraphentous; compare *M. islandica* subsp. *helvetica*, and something similar may be said of another diatom genus *Cyclotella*. The pennate diatom *Fragilaria crotonensis*, however, seems to be a typically eutraphentous species.

Some widely distributed genera within other taxonomic groups, such as Chrysophyceae, are no doubt significant for characterizing a lake. The genus *Dinobryon* thus includes two distinctly oligotraphentous species, *D. cylindricum* var. *palustre* and *D. bavaricum* var. *vanhoeffenii*, and one, *D. pediforme* characteristic for the dystrophic phase, while *D. divergens* is indifferent, and *D. sociale* var. *americanum* is eutraphentous according to my experience.

I should like to ask Dr. Brook: Do your experiences with the *Dinobryon* species of the Scottish lakes agree with this?

BROOK: Yes, they do agree on the whole. *Dinobryon divergens* certainly occurs in all types of Scottish waters from the richest to the poorest; *Dinobryon sociale* var. *americanum* seems always to be associated with fairly alkaline, and thus generally eutrophic waters, while *Dinobryon cylindricum* var. *palustre* occurs only in our oligotrophic Highland lochs.

DOUGLAS: Can you fit Esthwaite Water and Lowes Water, which we can consider as the most eutrophic of the English Lakes, into the table of these lakes which you showed.

BROOK: Recently I have received samples from Dr. LUND from these two lakes and an analysis of their plankton has shown that they fit into the end of my table. Thus they are the most eutrophic of the series as you suggest.

Extrait de la *Revue Algologique*, n° 3, Mars 1955.

The Aquatic Fauna as an Ecological Factor in Studies of the Occurence of Freshwater Algae [1]

■

In considering the factors which may influence the occurrence and periodicity of freshwater algae, emphasis is usually laid upon the physical and chemical environment and its variations. The possible effects of the aquatic fauna, whilst for a long time recognised, does not seem to have been given the attention which it deserves and in fact in many ecological studies, this factor has been ignored. It is the object of this paper to attempt to indicate its importance and to outline briefly observations and experiments which have been carried out in attempts to evaluate its significance, particulary in relation to the attached and bottom living algal flora.

That this biotic factor may at times be of over-riding importance was first brought to my attention when studying the algal flora of slow sand filter beds of waterworks. Since each of those eight filter were cleaned in turn once every 2 to 3 months, so that there were differences of at least two weeks to 2 to 3 months between the periods for which different beds had been in operation, they afforded an excellent opportunity for studying the establishment and colonization of the algal flora. Thus particular attention was paid to comparing the algal populations of beds which had been in operation for different lengths of time. Such comparisons showed that during many months of the year, the expected result, that algae were most plentiful in beds which had been in operation for the longest time, was observed. At other times, however, particularly between May and September, many species which were frequent, or even abundant, in recently cleaned beds were rare or absent in beds which had been in operation for longer periods.

(1) Cette note a fait l'objet d'une communication au VIII[e] Congrès international de Botanique de Paris, section de Phycologie.

This disappearance from « older » beds was most striking in the case of filamentous diatoms (*Melosira varians* Ag., *Fragilaria capucina* Desm. and *Diatoma vulgare* Bory.) and filamentous Chlorophyceae (*Spirogyra* and *Zygnema* spp.).

Consideration of the factors which might have produced these differences indicated that neither physical nor chemical factors could be responsible, but it was not until similar differences were produced in culture vessels in the laboratory that it was realised that the browsing of animals might be the cause. Sand and bottom-living algae from the filters were kept in these vessels and glass slides placed on the sand, weekly counts being made of the numbers of algae growing on them. Many algae which were at first numerous, became less frequent and in certain cases disappeared after two or three weeks. At the same time it was noticed that on some slides there were diatoms without cell contents or whose chromatophores were contracted, while other individuals of the same species appeared quite healthy. This applied particularly to unattached and typically bottom living diatoms (*Navicula, Nitzschia* and *Pinnularia* spp.). Later protozoa were observed with ingested diatoms in their bodies, and moreover, the ingested species were those which were disappearing. Clearly, the « loss » of certain algae from the vessels was due to the feeding of these protozoa. An attempt was therefore made to determine whether protozoa and/or other algae-eating animals could be producing a similar effect in the filters.

Although protozoa were found in the filters and they may in certain cases have reduced the numbers of pennate diatoms, particular attention was paid to the insect larvae, for many of these had been observed in the filters during the autumn of the previous year when many filamentous algae had disappeared from the « older » beds. Of these larvae, tube twelling Chironomids, Trichoptera and Ephemeroptera were abundant from April to October, and once each month, ten of each type of larvae were dissected and the gut contents examined. These dissections showed that these larvae were for the most part algal eating and that their food consisted primarily of the filamentous diatoms and Chlorophyceae which had disappeared from the older beds. Thus it was inferred that the browsing of the aquatic insect fauna was the factor responsible for the absence of these algae from the less recently cleaned filters, a fact later confirmed by laboratory observations.

Studies of the relationship between the aquatic fauna and the algal flora have been continued in Scottish lochs and it has been found that under natural conditions, as opposed to the essentially

artificial environment of the filters, similar effects due to browsing are apparent. In these studies the epiphytic flora of the macrophytes *Myriophyllum spicatum* L., *Eleogiton fluitans* (L.) Link, *Potamogeton natans* L. and *Littorella uniflora* (L.) Achers has been examined in relation to the feeding of the caddis larva *Leptocerus aterrimus* Stephens. Striking demonstrations of the disappearance of the diatom *Fragilaria capucina* and of filaments of *Bulbochaete* sp. from the epiflora of these plants through the feeding

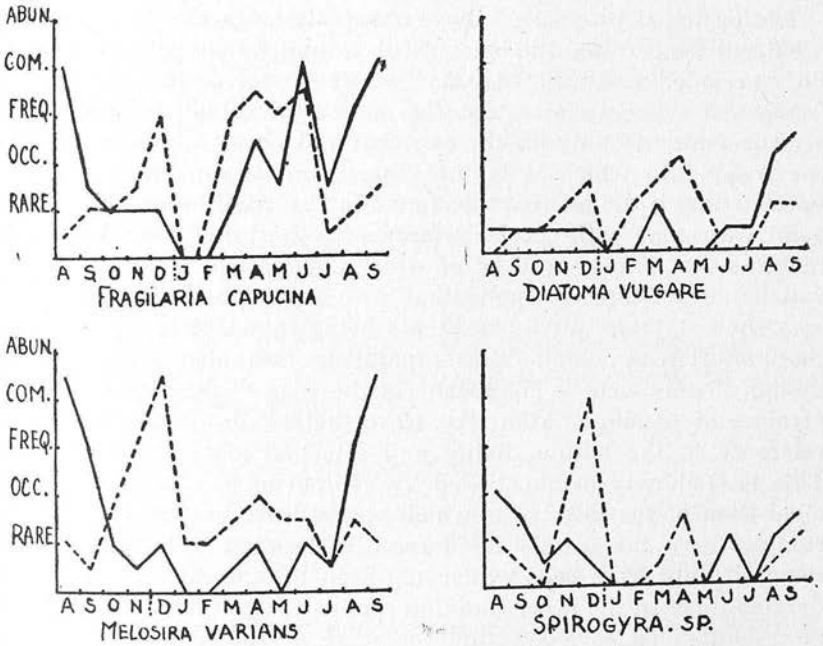

Fig. 1. — *Differences in the Amounts of Algae present in Filter Beds of Different Ages.*

Solid line = av. of two most recently cleaned ('newest') beds; broken line = av. of two least recently cleaned ('oldest') beds. Establishment successful when broken line is above the solid line.

of this (and possibly other) larvae have been observed. Whilst it is difficult to place such observations on a quantitative basis, preliminary laboratory experiments have shown that in the case of certain larvae, the removal of the epiflora by them can be rapid and complete. For example, it has been found that 10 larvae of the mayfly *Leptophlebia vespertina* (L.) can remove in four days, a dense algal felt consisting largely of *Achnanthes, Cymbella* and *Gomphonema* spp., *Tabellaria flocculosa* and *Bulbochaete* sp., from a strand of *Myriophyllum spicatum,* one foot in length.

Experiments have also been carried out to determine the extent to which protozoa can feed on freshwater algae (BROOK 1952) and it has been shown that certain species can eat considerable numbers of pennate diatoms, e. g. *Oxytricha* sp. feeding on *Nitzschia palea* can eat 90 diatoms per 24 hours. My own field observations and those of other investigators, notably GRAY (1952), indicate that this group of animals may play an important part in depleting bottom-living algal populations in streams and rivers, as well as in ponds.

The principal interest of these observations is their bearing on problems concerning the successful establishment of algae and their periodicity. FRITSCH (1931) in a survey of certain aspects of freshwater ecology states that the successful establishment of an alga depends not only on the physical and chemical properties of the water into which it is introduced, but in many cases may succeed only if the microscopic fauna is at a minimum. This latter point was made with special reference to the plankton, though he remarks that it may well be of wider application. My own observations sugget that its application with regard to the plankton is very limited, many phytoplanktonts being too large to be eaten by the majority of zooplankton organisms (see also LUND 1954), though it may well be significant in the case of the establishment of algae of nannoplankton size. Nevertheless, its application with reference to the bottom living and attached algal flora is clear. This is strikingly demonstrated by comparing the picture of the algal flora of the filter beds which would have been obtained had samples been taken only from recently cleaned beds on the one hand, or only from beds which had been in operation for a considerable time. In the accompanying graphs (Fig. 1) two curves have been plotted on each showing for some of the principal species, monthly differences in their abundance, one curve representing abundance in the two most recently cleaned and the other in the two least recently cleaned beds. It will be clear that had there been no animals browsing on these algae the curves for the « old » beds would always be above those for the « new ». However, for a considerable part of the year the abundance of these species in the « newer » beds is greater than in the « old ». In fact it is only in winter and early spring, when the aquatic fauna is at a minimum, that many algae seem able to establish themselves successfully. At other times they may be drastically reduced in amount, a reduction which can be correlated with the increasing effects of the browsing fauna.

It is instructive in the light of these findings to consider the results of other investigators who, in studying the periodicity of

freshwater algae have considered only physical and chemical variations as controlling factors. HODGETTS (1922) for example, in a four years study of a pond found that filamentous algae (Chlorophyceae) had periods of maximum abundance between March and May, with secondary maxima between October and January, while HOWLAND (1931) also showed that filamentous species were most abundant in the early part of each year, very few surviving after June. Clearly it is reasonable to suggest that the algae-eating fauna of these ponds was the main factor controlling the occurrence of filamentous algae. Moreover, it is well known that in two adjoining ponds which appear to be more or less identical in physical and chemical characteristics, marked differences may occurr in the composition of their algal flora. It seems probable that such differences may also be a reflection of differences in abundance of the fauna of such ponds.

The influence of the aquatic fauna in studies of the occurrence of freshwater algae cannot be ignored.

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10

NOTES ON SOME UNCOMMON ALGAE FROM LOCHS IN THE TUMMEL-GARRY CATCHMENT AREA.

BY

A. J. BROOK.

Notes on Some Uncommon Algae from Lochs in the Tummel-Garry Catchment Area.

By A. J. Brook.
(Brown Trout Research Laboratory, Pitlochry.)

(Read by title, 14th January 1954.)

In connection with work in progress at the Brown Trout Research Laboratory, Pitlochry, several lochs in the Tummel-Garry Catchment Area have been intensively studied. These are Lochs Choin and Cruinn (27/688679), Kinardochy (27/775550), Moraig (27/908666) and Lochan an Daim (27/718574).* From these a number of interesting species and varieties of algae have been identified with certainty and are therefore recorded here. Several are new records for Britain. The affinities of some others are obscure and require further study before being placed on record.

CHLOROPHYCEAE.

1. Chlamydomonas cingulata Pascher, var. seligeriensis Korschikoff. Pascher (1927), pp. 271–3, fig. 230*c*. (text-fig. 1, 1.)

An uni-algal culture of this *Chlamydomonas* was found, in May 1953, in a small rock pool on an island in Loch Kinardochy on which two families of gulls were nesting. The cells, which were mostly 18–20 μ l., 16 μ br., agree closely with the description given in Pascher (1927). A new British record.

2. Elakatothrix gelatinosa Wille.

Frequent at times in the plankton of Lochs Cruinn and Kinardochy. Cells mostly 14–16 μ l., 2·5–3 μ br.

3. Micractinium pusillum Fresen., forma quadriseta (Lemm.). (text-fig. 1, 2.)

Occasional in Loch Moraig. Previously recorded only from the plankton of Lough Beg, Ireland. Cells 8 μ diam., with "chlorococcoid" cell structure, and bearing four hollow bristles, each 16 μ l.

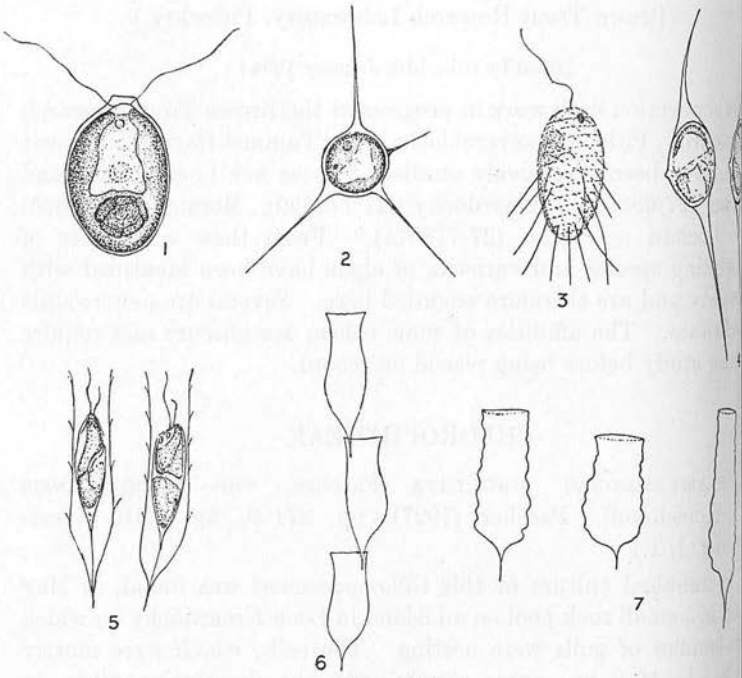
* The figures in brackets are normal National Grid references from the 1-inch Ordnance Survey of Scotland (1946), sheet 27.

4. Oocystis panduriformis West and West.

Common in Loch Cruinn.

5. Monostroma membranaceum W. and G. S. West.

Several well-developed plants taken in grab samples from t bottom of Loch Kinardochy at depths of five to fifteen feet; th



Text-fig. 1.

1. Chlamydomonas cingulata Pascher, var. seligeriensis Korschikoff. (×500.)
2. Micractinium pusillum Fresen., forma quadriseta (Lemm.). (×500.)
3. Mallomonas pallida Conrad. (×375.)
4. Diceras chodati Reverdin. (×500.)
5. Hyalobryon mucicola Pascher. (×500.)
6. Dinobryon sociale var. americanum (Brunn.) Bachm. (×250.)
7. Dinobryon crenulatum. (×375.)

were brought to the author's notice by Mr. W. R. Munro. There a only two previous British records of this alga.

6. Chaetonema irregulare Nowak.

Common at times on submerged glass slides in Lochs Kinardoch and Choin. Previously recorded only from W. Yorkshire (We 1912).

7. BOTRYOCOCCUS SUDETICUS Lemm.

Rare with *Botryococcus braunii* and *Stichogloea doederleinii* in Loch Choin. Cells 8 μ l., 6 μ br.

CHRYSOPHYCEAE.

8. STICHOGLOEA DOEDERLEINII (Schmidle) Wille.

Common at times in Lochs Kinardochy and Choin between May and October with *Botryococcus braunii*: maximum abundance in August. Although there is only one previous British record of this alga, it is probably common in summer in many Scottish lochs.

9. CHRYSOCHAETE BRITANNICA (Godward) Rosenberg. Rosenberg (1941).

Common on submerged slides in Loch Kinardochy, less abundant in Loch Choin. When this alga was first discovered by Godward (1933) in two pools near Epping Forest, she believed it to be a rare species. However, since then it has been found in Lake Windermere (Godward, 1937), in ponds near Richmond, Surrey (Lund, 1942), in filter beds in Northumberland (Brook—in the press) and now in these two Scottish lochs, which suggests that it has a wide and fairly general distribution throughout Britain.

10. MALLOMONAS PALLIDA Conrad. Huber-Pest. (1941), p. 99. Abb. 121. (text-fig. 1, 3.)

Occasional in Loch Moraig in March and early April. Cells mostly 15–16 μ l., 10 μ br., ellipsoidal with rhomboidal scales; spines only in posterior half of cell. One small, pale, disc-shaped chromatophore. Not previously recorded for Britain.

11. DICERAS CHODATI Reverdin. Huber-Pest. (1941), p. 209. Abb. 279. (text-fig. 1, 4.)

Quite common during early summer (May–June) in Lochs Cruinn, Kinardochy and Moraig. Cells usually 10–12 μ l., 6–8 μ br., with bristles of unequal length; mostly 15 and 25 μ l. No previous record for Britain.

12. HYALOBRYON MUCICOLA Pascher. (text-fig. 1, 5.)

Common in groups of 40–50 cells on submerged glass slides on an inorganic shore in Loch Kinardochy during May. This alga has been previously recorded from the British Isles only from Loch Earn.

Cells 16 μ l., 4 μ br., attached to envelopes by fine stalks 15–20 μ. Envelopes up to 8 μ br. and 40–50 μ l.

13. DINOBRYON BARVARICUM Imhof, var. MEDIUM (Lemm.) Kreig. Huber-Pest. (1951), p. 225, fig. 297.

With *D. barvaricum* in Loch Kinardochy. Envelope 56 μ, 7 μ br. A new British record.

14. D. SOCIALE Ehr. var. STIPITATUM (Stein) Lemm. Huber-Pest. (1941), p. 226, fig. 299.

Occasional with the type species in Lochan an Daim during period of great abundance in April 1953. Bachmann (1907) record this alga under the name *D. stipitatum* var. *elongatum* Imhof, from Lochs Lochy and Oich.

15. D. SOCIALE var. AMERICANUM (Brunn.) Bachm. Huber-Pest. (1941), p. 226, fig. 300. (text-fig. 1, 6.)

Common in Loch Moraig between March and early May. Occasional in Lochan an Daim in April. Envelopes measuring 30–40 μ l., 9–10 μ br. In Loch Moraig numerous cysts, 9 μ in diameter, were formed throughout April.

16. D. DIVERGENS Imhof. var. ANGULATUM (Seligo) Brunn. Huber-Pest. (1941), p. 229, fig. 303.

Rare, with the type species and *D. cylindricum* in Loch Kinardochy during autumn, winter and spring. Envelopes 40–50 μ l., 10 μ br.

17. D. SUECICUM Lemm. Huber-Pest. (1941), p. 216, fig. 288.

Very rare in Loch Kinardochy in January and February. Delicate envelope, 20 μ l., 4 μ br., with characteristic spiral sculpturing of wall. Lund (1952) has recently found the var. *longispinum* of this species in the Lake District.

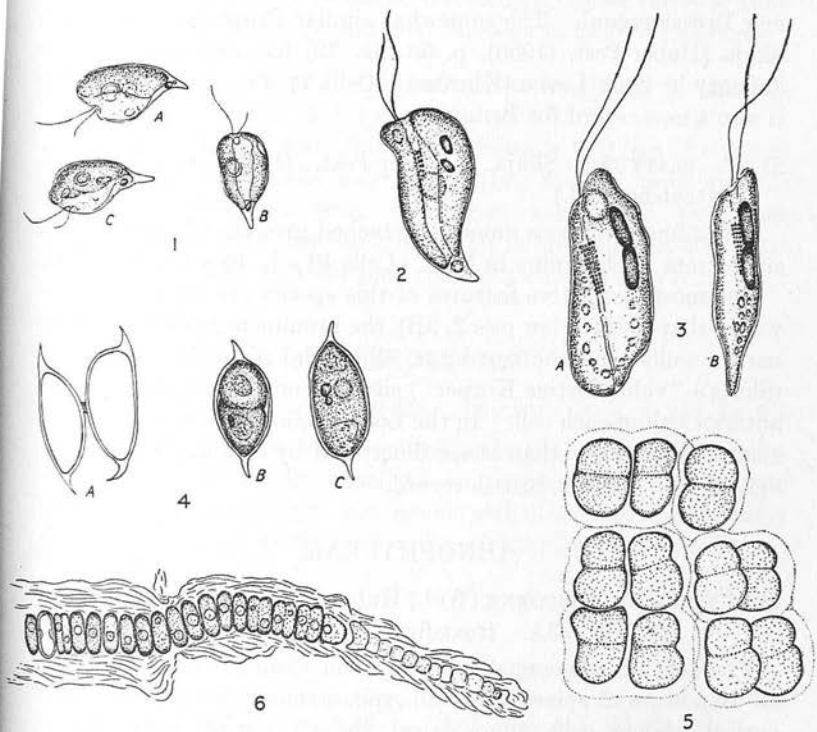
18. D. CRENULATUM. W. and G. S. West, *Naturalist*, Lond., 1905, p. 325, and figs. 7c and 7d. (text-fig. 1, 7.)

Common in December and January, and again in April and early May, in Loch Kinardochy. Always solitary. Total length of envelope varying from 24 to 36 μ. Breadth at base 6·5–9 μ (most 8 μ), narrowing slightly to 6–7·5 μ below lip at top of the envelope. The completely crenulate wall is a very distinctive feature.

CRYPTOPHYCEAE.

19. CHROOMONAS ACUTA Utermohl. Huber-Pest. (1950), p. 33, fig. 19. (text-fig. 2, 1.)

Abundant in Loch Kinardochy from January to March. Maximum of 4000 cells per ml. after disappearance of ice-cover on 21st



TEXT-FIG. 2.

1. CHROOMONAS ACUTA Utermohl.
2. CRYPTOMONAS EROSA Ehr. var. REFLEXA Marsson. (×500.)
3. CRYPTOMONAS PLATYURIS Skuja. (×375.)
4. CYSTODINIUM BICORNE (Wol.) Huber-Pest. (×375.)
5. MERISMOPEDIA MAIOR (Smith) Geitler. (×500.)
6. SCYTONEMA CRUSTACEUM Agardh. (×250.)

February. Also present during the same period in Loch Tummel. Cells spindle-shaped (7–10 × 4–5·5 μ), with a broad anterior end becoming narrow towards posterior end and ending in a characteristically curved, projecting tip, which persists even when the cells become mis-shapen when killed with formalin (see fig. 2, 1C). Gullet short. Flagella slightly smaller than length of cell. Pyrenoid

usually quite distinct, centrally placed on the dorsal side of the cell. Single chromatophore, olive green in colour. Movements rapid and usually erratic. A new British record.

20. CRYPTOMONAS EROSA Ehr. var. REFLEXA Marsson. Huber-Pest. (1950), p. 53, fig. 29. (text-fig. 2, 2.)

Very rare in Loch Moraig in spring. Cells 21 μ l., 11 μ br. A new British record. The somewhat similar *Cryptomonas marssonii* Skuja (Huber-Pest. (1950), p. 58, fig. 39) has also been found in January in Loch Leven (Kinross). Cells 24–39 μ l., 12 μ br. This is also a new record for Britain.

21. C. PLATYURIS Skuja. Huber-Pest. (1950), p. 57, fig. 34 (text-fig. 2, 3.)

A few fine specimens amongst attached growths of algae on glass slides from Loch Cruinn in May. Cells 40 μ l., 16 μ br., 10 μ thick.

The most distinctive features of this species are the more or less wedge-shaped side view (see 2, 3B), the prominent trichocysts in the narrow gullet and the two large, ellipsoidal metachromatic bodies (Skuja's "volutinartige Korper") situated on the dorsal side in the anterior half of each cell. In the Loch Cruinn specimens these were considerably larger than those illustrated by Skuja (1948, Taf. 37 figs. 37–38). A new British record.

DINOPHYCEAE.

22. CYSTODINIUM BICORNE (Wol.) Huber-Pest. Huber-Pest. (1950) p. 299, fig. 293A. (text-fig. 2, 4.)

Frequent on submerged slides in Loch Cruinn. Cells 25–30 μ l. 12–16 μ br., with spines 35–40 μ l., spines usually 5–7 μ l., frequently curved. Some cells symmetrical though mostly asymmetrical, containing numerous brown chromatophores. No sign of furrows in vegetative cells, but these appear as the protoplast contracts before division (see 4B). Two large vacuoles at each end of the cell in which there is a constant, and very rapid movement of fine granular material. A new British record.

CYANOPHYCEAE.

23. MERISMOPEDIA MAIOR (Smith) Geitler. Geitler (1932), p. 265 fig. 130. (text-fig. 2, 5.)

Rare in plankton of Loch Choin. Small colonies, 8–16 cells. Cells 8–10 μ, vivid blue-green in colour with homogeneous contents. Cells

in groups of 4, each group being surrounded by a distinct mucilage envelope and thus clearly separated from one another, a characteristic which seems to distinguish this species from *M. elegans* A. Br. Geitler (1932) seems to question Smith's (1920) statement about the absence of a mucilage envelope ("ohne (*immer*?) Spezialhullen") which is unquestionably present in the Loch Choin specimens. Though not previously recorded for Britain, Lund (private communication) states that he has seen this alga in Lake Windermere.

24. SCYTONEMA CRUSTACEUM Agardh. Geitler (1932), p. 782, figs. 503–4. (text-fig. 2, 6.)

Common on stones with *Tolypothrix tenius* in 1–2 feet of water in Loch Kinardochy. Cells mostly 10 μ br., 4–8 μ l., with marked constrictions between cells. Trichomes surrounded by stout, irregular lamellar mucilage sheath varying in breadth from 20 to 30 μ. Heterocysts slightly broader than cells of trichome (11 μ br., 7 μ l.).

HETEROKONTAE.

25. HETEROCOCCUS VIRIDIS Chodat. Pascher (1925), p. 113, fig. 92.

Frequent with *Chrystochaete britannica* in Loch Kinardochy. Small flat plates of cells, usually 4–12 per plate, outer margins of cells rounded, inner margins contiguous with other cells and distinctly angular. Cell walls thick, each cell 8–10 μ br., with several brown, lobed chromatophores.

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11

NOTES ON SOME UNCOMMON ALGAE FROM LOCHS IN KINROSS, PERTHSHIRE AND CAITHNESS.

BY

A. J. BROOK.

Notes on Some Uncommon Algae from Lochs in Kinross, Perthshire and Caithness.

By A. J. Brook.
(Brown Trout Research Laboratory, Pitlochry, Scotland.)

(Read by title, 16th December 1954.)

The following notes relate to algae found during the course of researches carried out at the Brown Trout Research Laboratory, and, as with those reported in an earlier communication (Brook, 1954), they are all either new records for, or of rare occurrence in, the British Isles. The locality of the lochs mentioned is indicated by the full National Grid Reference, given after each is named in the text for the first time.

ISOKONTAE.

Chlorococcales.

1. Characium limneticum Lemm. (Text-fig. 1, 1.)

Frequent on the filtering combs and in the body cavities of *Daphnia hyalina* var. *lacustris* Leydig in Loch Moraig, Perthshire (27/908666), during June and July. Whilst many typical specimens regularly fusiform and lunate in outline have been observed, many short cells of irregular shape were also found. Often groups of cells tend to form fan-shaped clusters within the body cavity. Cells 40–90 μ l., 6–9 μ br. Also present in the summer plankton of Loch Shurrery, Caithness (39/044555).

2. Pediastrum kawraiskyi Schmidle. (Text-fig. 1, 2.)

A form differing from the type species in the possession of clathrations between the inner cells, and also in having granular cell walls, was rare in plankton samples from Loch Shurrery collected in May 1950. All coenobia were 32-celled, with cells 15–25 μ diam.

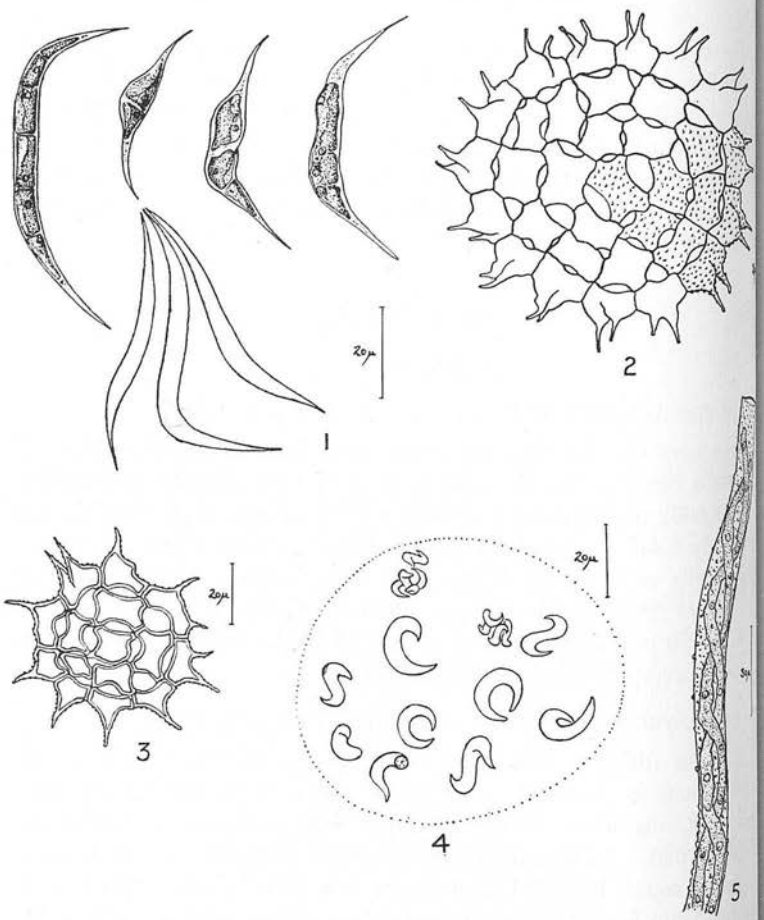
An unusual 15-celled *Pediastrum* coenobium was found in a sample from Loch Shurrery taken in September 1950 (text-fig. 1, 3). In this, the inner cells were quadrate, with lens-shaped spaces between them, while the peripheral cells were of three types:

(*a*) 4 cells with outer margins extended to form a single projection, as in *P. simplex*;

(*b*) 4 cells showing various stages in the development of a secon process (cf. *P. duplex*);

(*c*) 1 cell with two fully developed projections, but which are no lying in the same plane, as in *P. kawraiskyi*.

Dr. Gunnar Nygaard, to whom drawings of this individual have bee shown, has commented: "At first I considered it to be a teratologic form, but alternatively it may be a colony subjected to very variabl



TEXT-FIG. 1.

1. CHARACIUM LIMNETICUM Lemm.
2. PEDIASTRUM KAWRAISKYI Schmidle.
3. PEDIASTRUM sp. (see text).
4. KIRCHNERIELLA LUNARIS var. IRREGULARIS G. M. Smith.
5. GENICULARIA ELEGANS West & West.

environmental factors, perhaps extreme life conditions. If one assumes the latter, this colony seems to indicate that the number of processes on the peripheral cells is a character of but little taxonomic value, apparently a mere modification."

3. LAGERHEIMIA GENEVENSIS Chod.

Occasional in the winter plankton of Loch Leven, Kinross (37/145020); maximum in January of 30 cells per ml.

4. KIRCHNERIELLA LUNARIS var. IRREGULARIS G. M. Smith. (Text-fig. 1, 4.)

Rare in the plankton of Loch Shurrery in June and July 1950. Cells up to 15 μ l. and 5 μ br., with apices characteristically twisted (see Prescott, 1951, p. 258 and pl. 58, fig. 4). A new record for Britain.

5. BOTRYOCOCCUS PROTUBERANS West & West.

Frequent in Loch Chaluim, Caithness (39/022519), in June and July. Previously recorded only in plankton from lochs in the Hebrides (West and West, 1905; Lind, 1952).

CHAETOPHORALES.

1. DICHRANOCHAETE RENIFORMIS Hieron.

Small numbers of this alga have been found attached to glass slides throughout the year in Lochs Choin (27/688679), Kinardochy (27/775550) and Dunmore (27/921590).

CONJUGATAE.

1. GENICULARIA ELEGANS West & West. (Text-fig. 1, 5.)

Occasional filaments of this alga, previously recorded only from the plankton (see West and Fritsch, 1932, p. 241), have been found from time to time attached to *Myriophyllum spicatum* in Loch Dunmore, some filaments consisting of as many as 9 cells. Cells mostly 16·5 μ br., though sometimes as narrow as 13·5 μ, increasing to 17·5 μ (a few to 20 μ) at the apices; cells 290–400 μ l. Never more than 2 chloroplasts per cell observed, and usually making 3 turns of the cell. Cell walls for the most part densely and minutely granulate, but differing from original description (West and West,

1904, p. 36, pl. v, figs. 1 and 2) by the presence of coarse, irregular disposed granules on all cell walls.

2. STAURASTRUM PSEUDOPELAGICUM West & West. (Text-fig. 2,1

An unusual specimen of this desmid was found in the plankton Loch Shurrery in July 1950. This desmid was originally describe (West and Carter, 1923, p. 107) as possessing semicells whose angl are produced to form short, stout, diverging processes tipped wi 2 strong diverging spines, though they record (p. 108) that G. Smith observed some British specimens with 3 spines. The Lo Shurrery plant had processes in one semicell tipped with 2 spin and in the other with 3 spines.

CHRYSOPHYCEAE.

1. OCHROMONAS VERRUCOSA Skuja (see Huber-Pestalozzi, 19 p. 171, Taf. XLI, Abb. 230a).

A few individuals amongst filamentous algae from Loch Choin September. Cells 22–25 μ l., 18–19 μ br. A new British record.

2. CHRYSOSPHAERELLA LONGISPINA Lautb.

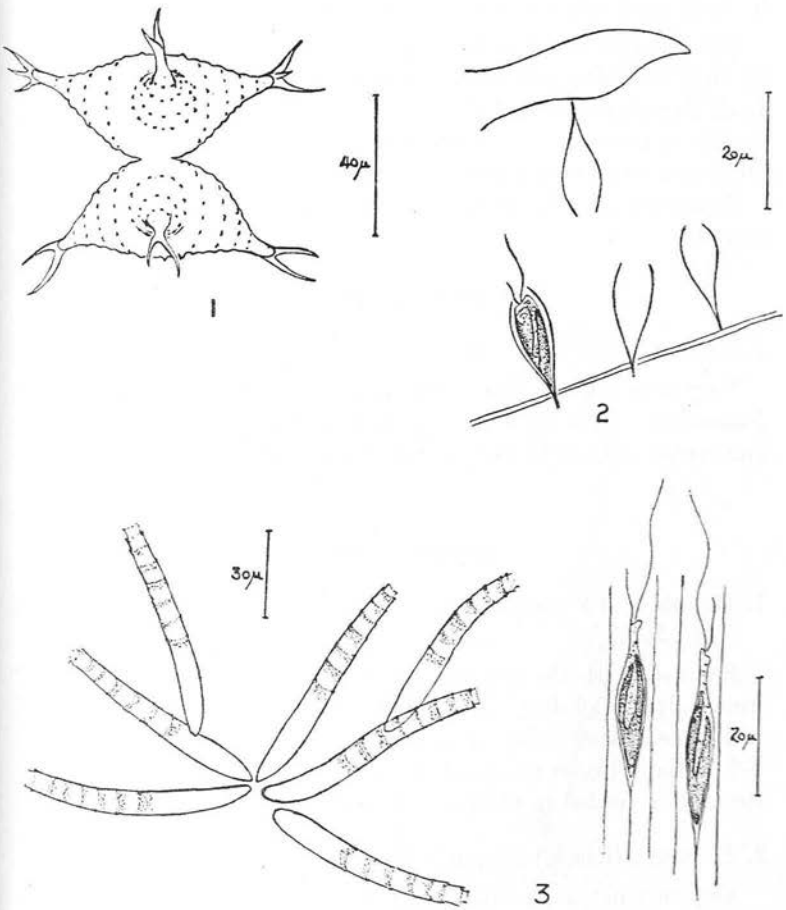
Rare to occasional throughout the year in Loch Dunmore, thou most frequent in November and December when the plankt consists mainly of Chrysophyceae, dominated by *Synura uvella* a *Uroglena americana*, but in which *Eudorina elegans* and *Botryococ braunii* are also abundant. Although Conrad (1941) and Sku (1948) record this alga as a summer or autumn species, it is interest to note that it persisted even under ice in Loch Dunmo when water temperatures were between 1–3° C., a fact which te to confirm Lund's view (1949) that the chemical constitution of t water is probably more important than temperature in influenc the seasonal distribution of the Chrysophyceae. Colonies usua 40 μ diameter without processes, which are from 25–30 μ l.; c 8–10 μ diam. Cyst formation observed in sample collected un ice in January; cysts 12·5 μ diam.

3. DINOBRYON UTRICULUS var. ACUTUM Schiller. (Text-fig. 2, 2)

Frequent on filaments of *Oedogonium punctato-striolatum* and oth *Oedogonium* spp. in Loch Choin between June and October. O individual found on envelope of *Dinobryon sertularia*. Envelop 20–22 μ l., 6·5–7·5 μ br. A new British record.

4. HYALOBRYON RAMOSUM Lautb. (Text-fig. 2, 3.)

Large colonies present on glass slides from Loch Choin, Loch Dunmore and Lochan an Daim more or less throughout the year.



TEXT-FIG. 2.

1. STAURASTRUM PSEUDOPELAGICUM West & West.
2. DINOBRYON UTRICULUS var. ACUTUM Schiller.
3. HYALOBRYON RAMOSUM Lautb.

The "growth rings" on the envelopes of this alga are very indistinct in living or unstained material, and can only be seen clearly by staining with methylene blue. Lauterborn's original drawing (see Huber-Pestalozzi, 1941, Taf. LXXI, Abb. 327a) indicates that these

"rings" are all markedly flared out from the envelope. In th Scottish plants, however, this only applies to the uppermost 2 o 3 rings, the older, lower ones lying close to the envelope.

5. PSEUDOKEPHYRION UNDULATUM (Klebs) Pascher.

Groups of 10 to 12 individuals have been found loosely attache by their posterior ends to glass slides, with *Hyalobryon ramosum*, i Loch Dunmore between November and February. While attache to this substratum the individuals swayed gently from side to sid but swam away very actively when detached.

Envelopes 25 μ l., 15 μ br.; 7 μ br. at mouth. A new Britis record.

DINOPHYCEAE.

1. CYSTODINIUM STEINII Klebs.

Very rare among *Myriophyllum spicatum* in Loch Dunmore i November. Cells 75 μ l., 30 μ br.; protoplast with well-marke transverse and short longitudinal furrows; 62 μ l., 27 μ br.

MYXOPHYCEAE.

1. CHROOCOCCUS LIMNETICUS var. DISTANS G. M. Smith. (Tex fig. 3, 1.)

Frequent with the type species in the plankton of Loch Shurrer from July to October. This variety differs from the species by it widely separated cells, or groups of cells. The cells are mostl 7–8 μ diam. (some up to 12 μ), with well-defined sheaths 1 μ b Recently recorded from Wales (Woodhead and Tweed, 1954).

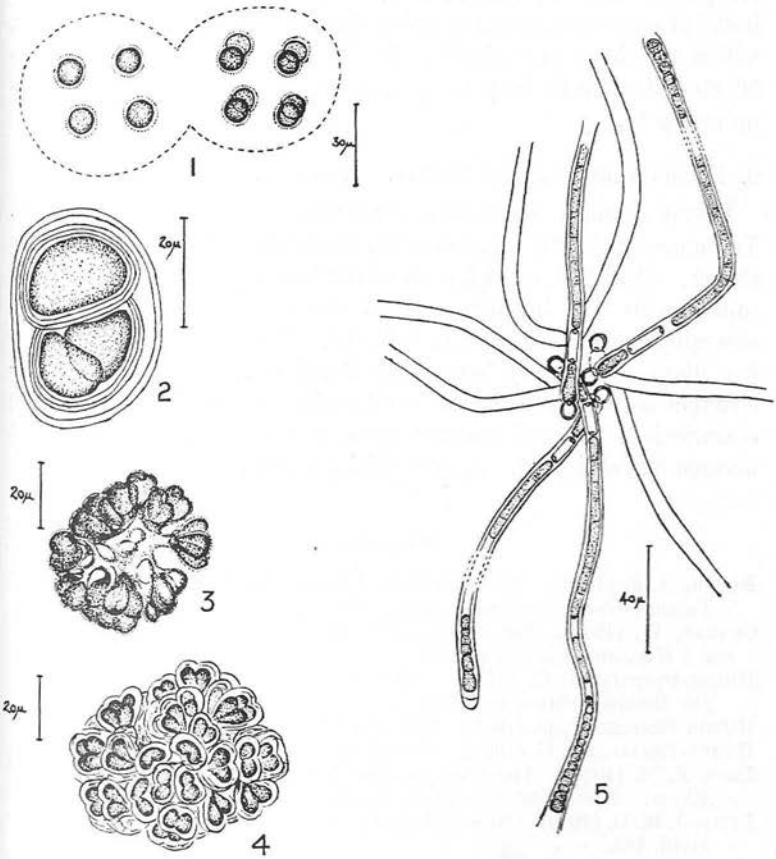
2. C. TENAX (Kirch.) Hieron. (Text-fig. 3, 2.)

Very rare in the plankton of Loch Scye, Caithness (39/005555), i July. Colony 45 μ l., 30 μ br., with cells 12–15 μ diam. Sheath enclosing individual cells very strongly lamellate, 2·5 μ thick lamellae of outer sheath enclosing groups of cells less distinct an up to 4·5 μ thick. A new British record.

3. GOMPHOSPHAERIA APONINA var. CORDIFORMIS Wille. Tex fig. 3, 3.)

Rare in the plankton of Loch Shurrery during July and Augus with the type species. Cells heart-shaped and borne at the ends o

distinct, stout, radiating gelatinous strands. Colonies 45 μ diam., with cells 6 μ br., 9 μ l. A new British record.



TEXT-FIG. 3.

1. CHROOCOCCUS LIMNETICUS var. DISTANS G. M. Smith.
2. CHROOCOCCUS TENAX (Kirch.) Hieron.
3. GOMPHOSPHAERIA APONINA var. CORDIFORMIS Wille.
4. GOMPHOSPHAERIA APONINA var. DELICATULA Virieux.
5. MICROCHAETE TENERA Thuret.

4. G. APONINA var. DELICATULA Virieux. (Text-fig. 3, 4.)

Also rare in Loch Shurrery in July and August. The identification of this variety, which is a new British record, has kindly been confirmed by Dr. G. Nygaard. He recorded this variety in material from South Africa (Nygaard, 1932), and his illustrations agree closely with the present plants (see also Huber-Pestalozzi, 1938,

Taf. XIII, Abb. 39d). Dr. Nygaard writes: "The measurements o the cells agree very well with those given by Geitler in Rabenhorst Kryptogamenflora (1932, p. 246). The special teguments (speziel hulle) of your specimens are rather thick, a character lying, howeve within the limits of variability for this blue green alga." Colonie 50–80 μ diam., cells 7·5 μ l., 4 μ br. and enclosed in mucilage sheath up to 2 μ br.

6. MICROCHAETE TENERA Thuret. (Text-fig. 3, 5.)

Found amongst filamentous algae from Loch Choin in Octobe Trichomes up to 700 μ l., 7·5 μ br., including their distinct mucila sheath. Cells 7–8 μ l., 4·5 μ br. at the base of the trichome, rapidl tapering to 3 μ br. for most of the remaining length thoug enlarging again at the apex to 6–7 μ br. Basal heterocysts spheric 6 μ diam., intercalary heterocysts 3·5 μ br., 12–13 μ l. No con striction between cells in the basal region of the trichomes, thoug constrictions are well marked towards the apex, where the cel become barrel-shaped. A new British record.

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12

Notes on Freshwater Algae, mainly from Lochs in Perthshire and Sutherland

A. J. BROOK

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Notes on Freshwater Algae, mainly from Lochs in Perthshire and Sutherland.

By A. J. Brook
(Brown Trout Research Laboratory, Pitlochry).

(Read by title, 14th June 1956.)

As in the case of two earlier notes on Scottish freshwater alga (Brook, 1954, 1955), all the species discussed in the present communication either are of rare occurrence, or are new record for Scotland and, in some cases, for the British Isles. The locality of each loch mentioned is indicated by the full National Grid Reference, given after it is named in the text for the first time.

The author wishes to express his thanks to Dr. H. D. Slack of the University of Glasgow who collected many of the samples containing interesting material; also to several of his colleagues who have sampled lochs in Sutherland.

ISOKONTAE.

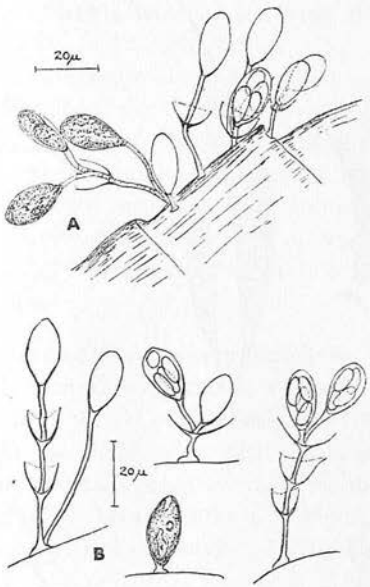
Volvocales.

1. Characiochloris epizootica (Korschik.) Pascher (Text-fig. 1).

Pascher (1927), p. 486-7, and fig. 442. Skuja (1948), p. 104, Pl. 8, figs. 22-27.

Present on occasional individuals of *Diaptomus gracilis* in summer in Loch Choin, North Perthshire (27/688679) and on others from Loch Chon, near Aberfoyle, S.W. Perthshire (27/420050).

This alga grew abundantly on *Diaptomus* in laboratory cultures from material collected from Loch Choin, and its identity was kindly confirmed from this material by Prof. H. Skuja who considered it to be the most luxuriant development of this organism that he had seen. In this material, and in that from Loch Chon, Aberfoyle, there was a marked tendency for new individuals to remain and develop within the cup-shaped lower half of the old, empty mother cells. Two or even three of the tetrad of daughter cells which arise from each mother cell may develop in this position (Text-fig. 1, A). In addition a succession of individuals may arise within these old cups, the remains of four generations, one within the other, often being present (Text-fig. 1, B.)



TEXT-FIG. 1.

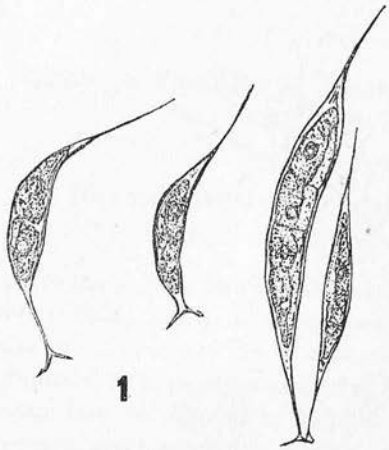
1. CHARACIOCHLORIS EPIZOOTICA (Korschik.) Pascher.
   A. Group of individuals on *Diaptomus gracilis* from Loch Chon, Aberfoyle, showing development of new cells within remains of old mother cells.
   B. Specimens from Loch Choin, N. Perthshire, showing development of successive generations within mother cell remains.

The cells range from 4 to 12·5 μ br. and from 7 to 25 μ l. Their mucilage stalks may be as long as 50 μ, though usually they are much shorter (15-25 μ l.).

CHLOROCOCCALES.

1. CHARACIUM GRACILIPES Lambert (Text-fig. 2, 1).

A frequent epiplankter on *Daphnia hyalina* from Loch Laggan, near Fintry (26/625925) and Lochan Geal, to the north of Loch Lomond (27/318163), with *Colacium vesiculosum* Ehrb. It has been observed that while the base of most of the cells is attenuated to form a long, slender, filiform stipe with a typically branched end which serves for attachment, the stipe may sometimes be absent, the branched base developing directly from the body of the cell. Cells 50-75 μ l., 5-8 μ br.



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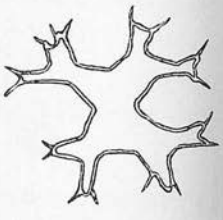

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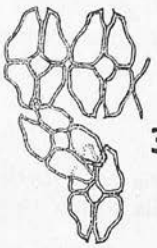

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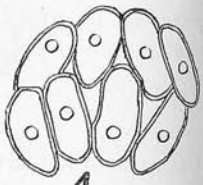

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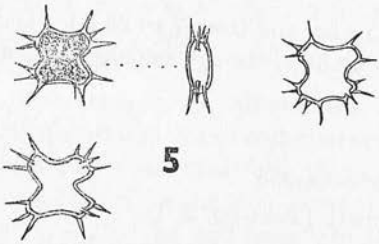

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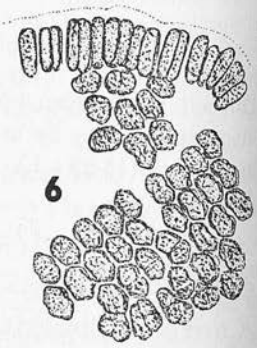

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20μ

2 TETRAEDRON GRACILE (Reinsch) Hansgirg (Text-fig. 2, 2).
(See Smith (1920), p. 122, Pl. 26, figs. 1-5.)

Rather stouter and more angular specimens of this alga than those hitherto described were present in small numbers in the summer plankton of Loch Shurrery, Caithness (39/044555). Nevertheless, the twice-branched angles of the cells, producing the narrowing processes which end in minute spines, and the fact that the primary branchings are at an angle of 90° with one another and parallel with the sides of the cells, confirms the identity of this alga.

3. CLOSTERIOPSIS LONGISSIMA var. TROPICA W. & G. S. West.

Present in the summer plankton of Loch na Beiste Brice, Sutherland (29/238501). Cells mostly 90-100 μ l. and 5 μ br. tapering to 2 μ at the ends, each with a single chloroplast containing 5 or 6 pyrenoids. Since it was first described from the Shetlands (W. & G. S. West, 1905) it is believed that this alga has not been recorded from elsewhere in the British Isles.

4. CRUCIGENIA PULLOIDEUM (Teiling) nov. comb. (Text-fig. 2, 3).
(=*Tetrastrum pulloideum* Teiling, Bot. Notiser, 1942, p. 66, fig. 2.)

Cells quadrately arranged, with groups adhering to form syncoenobia consisting usually of 16, or more rarely, 24 cells. Bases and middle third of the inner sides of each cell in mutual contact and in consequence flattened. Apices of cells tapering to minute points (apiculi) which in the present material would seem to be more delicate than those depicted by Teiling (1942). Adjacent apiculi pointing inwards, towards one another as in *Crucigenia apiculata* Schmidle, though differing from this species in that the outer cell faces are markedly concave, thus resembling *Crucigenia crucifera* (Wille) Collins and *C. truncata* Smith. Cells 4-8 μ l., 3-6 μ br. Coenobia 9-16 μ l., 6-12 μ br.

TEXT-FIG. 2.

1. CHARACIUM GRACILIPES Lambert.
2. TETRAEDRON GRACILE (Reinsch) Hansgirg.
3. CRUCIGENIA PULLOIDEUM (Teiling) nov. comb.
4. SCENEDESMUS ARCUATUS Lemm.
5. ISTHMOCHLORON TRISPINATUM (West & West) Skuja.
6. HOLOPEDIA GEMINATA Lagerh.
7. OSCILLATORIA SPLENDIDA Grev. forma.

Since these plants show clear affinities with the above-mentioned *Crucigenia* species and in addition regularly form syncoenobia, it seems reasonable to transfer this species from the genus *Tetrastrum* to *Crucigenia*.

Rare with *Crucigenia minima* Brunn. in the summer plankton of Loch an Daimh Beg, Sutherland (29/163428).

5. Crucigenia tetrapedia (Kirchn.) W. & G. S. West.

Occasional in the plankton of Lochan Spling, Perthshire (27/503004). The square coenobia were mostly 8 μ br.

6. Scenedesmus arcuatus Lemm. (Text-fig. 2, 4.)

Frequent in the plankton of Littleton and Waulkmill Reservoirs (26/524579), Renfrewshire. Curved coenobia consisting of 8 cells 10-18 μ l., 4-7·5 μ br., alternately arranged in a double row. Cells somewhat flattened where they join one another, and with small, though distinctive intercellular spaces between each. Coenobia 20-28 μ br., 22-35 μ l.

HETEROKONTAE.

1. Isthmochloron trispinatum (West & West) Skuja (Text-fig. 2, 5). (= *Arthrodesmus trispinatus* West & West.)

Occasional in the spring plankton of Loch an Daimh Mor, Sutherland (29/159432). This alga was originally described from N. Ireland by W. & G. S. West (1902) and named *Arthrodesmus trispinatus*. (It is also figured from African material by Fritsch and Rich, 1937, p. 203, and Fig. 20B). Since the Wests' description was based on fixed material which did not allow the exact nature of the chloroplasts to be determined, they conceded that the alga might, however, be one of the Chlorococcales belonging to the genus *Tetraedron* rather than a desmid. It was in fact renamed later *Tetraedron trispinatum* by Huber-Pestalozzi (1938) (see also Teiling, 1946, fig. 7). However, Skuja's recent critical study (1948) of this plant indicates that it should in fact be regarded as a heterokont. In agreement with Skuja's description the corners of these tetrahedral cells may be tipped with a very variable number of spines which in the Sutherland plants may be from 2 to 5. (Skuja, Pl. XXXVI, figs. 9-11, indicates 6 in some cases.) Moreover, these spines do not all lie in the same plane.

CHRYSOPHYCEAE.

1. MALLOMONAS ELONGATA Reverdin.

Rare in the plankton in the southern basin of Loch Lomond (26/390890). Cells mostly 75-80 μ l., 17·5 μ br. It is believed that this alga has not previously been recorded in Britain.

2. HYALOBRYON POLYMORPHUM Lund.

This chrysophycean was first described by Lund (1953) as an epiplankter on the cells of various planktonic algae from several of the English Lakes. It has now been observed with *Salpingoeca frequentissima* (Zach.) Lemm. on *Asterionella formosa* Hass.; also on *Eucapsa alpina* Clem. & Shantz and on *Gemellicystis neglecta* Teiling em. Skuja, from Loch Kinardochy, Perthshire (27/775550). The latter alga also carried *Salpingoeca* and some individuals were at the same time parasitized by the chytrid *Rhizophydium fulgens* Canter. Lund (private communication) has suggested that the alga referred to as *Hyalobryon mucicola* Pascher (Brook, 1954, p. 209, Fig. 1, 5) and which was present in considerable numbers on glass slides which had been submerged in this loch, is also *H. polymorphum*.

Dinobryon tabellariae (Lemm.) Pascher has been found in small numbers on *Asterionella formosa* from Loch Freuchie, Perthshire (27/865375).

BACILLARIOPHYCEAE.

1. MELOSIRA GRANULATA var. ANGUSTISSIMA O. F. Müll.

Very abundant in the highly eutrophic Lindores Loch (Fife) (37/265165) (in May, pH 8·7, alkalinity 70 p.p.m. $CaCo_3$, total hardness 99) in July, with a bloom of *Anabaena planctonica* Brunn. and persisting until September. The identity of this alga has been kindly confirmed by Dr. J. W. G. Lund. Lund (1954) has pointed out that *Melosira granulata* is widespread in lakes and reservoirs in the lowlands of England but is absent from lakes and tarns in the English Lake District. There would appear to be no authentic records of this diatom for Scotland for although the Wests listed it from Loch Lomond, Lund's re-examination of their material has shown it to be in fact *M. italica subarctica*. During the past year a considerable number of plankton samples from Loch Lomond have been examined by the author and once again only the latter species has been encountered.

2. CYCLOTELLA GLOMERATA Bachmann

Lund (1951) has recorded this diatom from the plankton of 19 bodies of freshwater in the English Lake District, and it has also been recently recorded from Wales by Woodhead and Tweed (1954a). Small groups of this very small diatom, usually consisting of not more than 4 cells, have now been found in Sutherland in Loch a' Bhadaidh Darraich (29/167445), Loch Borralie (27/382670) and Loch an Daimh Beg; in Inverness in Loch Morlich (28/965095) and Loch Pityoulish (28/920135); from Loch Leven, Kinross (37/145020); and in Perthshire from Loch Bhac (27/822622), Loch Kinardochy, Loch na Craig (27/883455), Loch of Craiglush (37/043443), Loch Kennard (27/905460), Loch of Lowes (37/050440), and Loch Skiach (27/950475).

Maxima in early May, 1956, of 7880 and 1380 cells per ml have been recorded from Loch Kinardochy and Loch Skiach respectively. The average colony size of these populations was approximately four cells, and the largest was eighteen cells.

CYANOPHYCEAE.

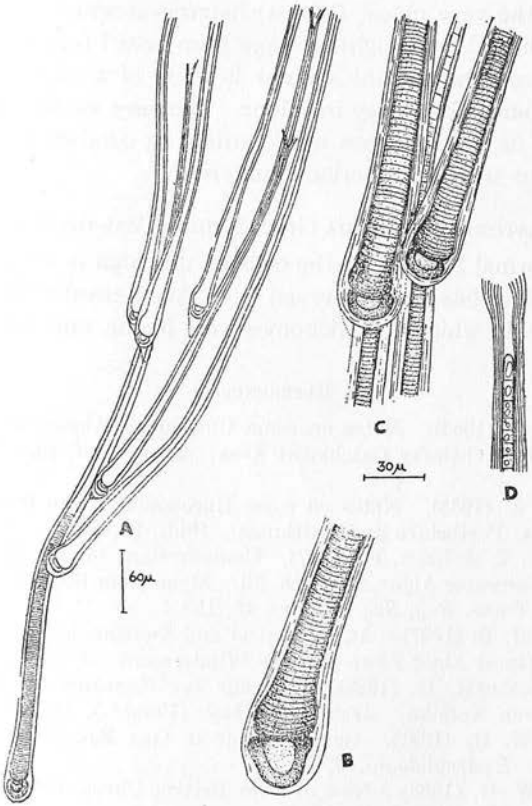
1. HOLOPEDIA GEMINATA Lagerh. (Text-fig. 2, 6.)

Rare amongst a bloom of *Oscillatoria limosa* Ag. in the eutrophic Auchterarder House Loch, Perthshire (27/958150) (pH 8·2, alkalinity 108). Colonies in the form of curved plates of more than 100 μ diameter. Cells 5 μ br. and 8-9 μ l.; mostly angular in surface view where mutually adpressed.

2. DICHOTHRIX BAUERIANA var. CRASSA Godward (Text-fig. 3).

This variety of *D. baueriana* was first described from Windermere (Godward, 1937, p. 562, fig. 21 A-E) and it would appear to have been recorded from no other part of Britain. Recently, however, considerable amounts have been found attached to various substrata in Loch an Daimh Mor, Sutherland. On occasions considerable amounts appear to have become detached, for well developed plants have been quite frequent in plankton samples.

The trichomes of the alga, which are for the most part about 15 μ br. tapering to 5 μ at their tips and swelling to 25-29 μ in breadth at their base, are enclosed in a firm, thick and distinctly stratified mucilage sheath, usually about 5 μ br. The sheaths are brown in colour in the basal region, becoming yellow towards



TEXT-FIG. 3.

1. DICHOTHRIX BAUERIANA var. CRASSA Godward.
   A. Detached plant from a plankton sample.
   B. Lowest (oldest) filament of a plant showing a typical cup-shaped heterocyst.
   C. Typical younger filaments with bean-shaped heterocysts.
   D. Tip of filament with narrowed, vacuolated trichome and showing separation of layers of the sheath.

the tips. The considerably narrower vacuolated cells in the tip of the trichome are up to 8 μ l., and in this region the layers of the enclosing sheath tend to separate, becoming markedly flared out at the end of each filament. The heterocysts tend to be broader than in the Windermere plants, being 22-25 μ br. and 15 μ l. in the older parts. However, in agreement with Godward's description they are mostly distinctly bean-shaped, except some-

times for the very oldest (lowest) heterocyst which may be cup- or dome-shaped, and slightly longer than broad (see Fig. 3A). In most heterocysts, the thick outer layer is of a vivid blue while the inner part is blue-grey in colour. The very swollen mucilaginous bases of the branches as described by Godward are not so conspicuous in the Sutherland material.

3. OSCILLATORIA SPLENDIDA Grev. forma (Text-fig. 2, 7).

The normal breadth of the cells of this alga is from 2-3 μ. A form however has been observed from Auchterarder House Loch, Perthshire, in which the trichomes were 5 μ br. and 6-8 μ l.

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Notes on Algae from the Plankton of some Scottish Freshwater Lochs

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Notes on Algae from the Plankton of some Scottish Freshwater Lochs.

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(Received 24th May 1957)

The following notes deal with algae which have been found in collections of phytoplankton taken with a tow net of 180 meshes to the inch. Most of the algae considered are new records for Scotland and a number do not seem to have been found previously in the British Isles. The locality of each loch mentioned is indicated by the full National Grid Reference, given after it is named in the text for the first time.

CHLOROPHYCEAE.

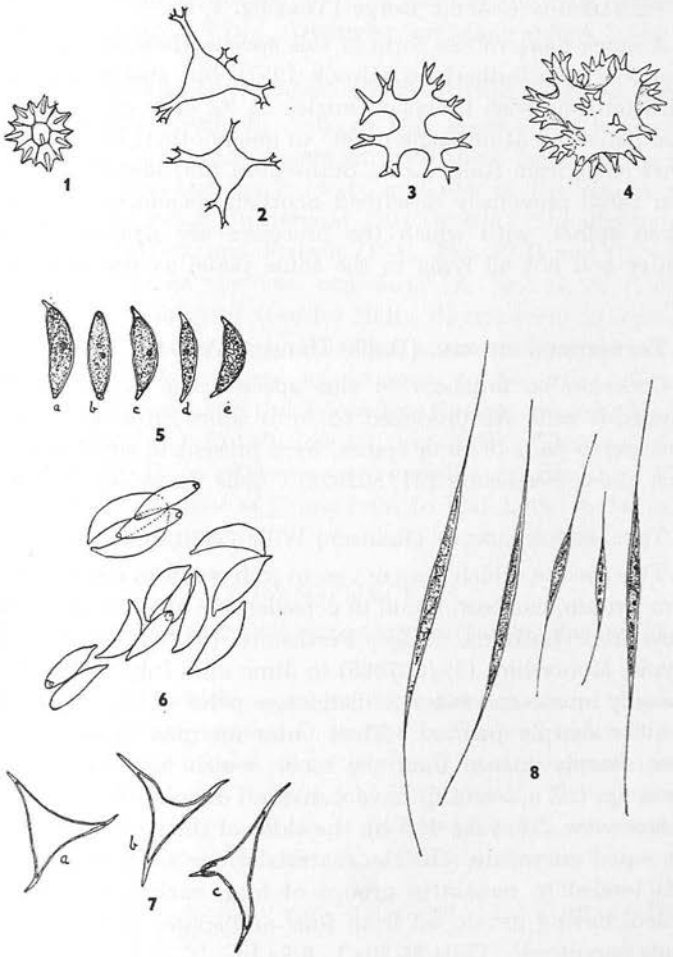
Chlorococcales.

1. Pediastrum tetras var. tetraödon (Corda) Rabenh. (Text-fig. 1, 1).

Specimens of this variety have been found in summer samples of plankton from Loch Moraig, Perthshire (27/908666). The coenobia are always 8-celled and the outer margins of the seven peripheral cells are very deeply incised. The resulting lobes are further divided to form sharply pointed, divergent, horn-like processes, which in the present material tend to overlap the adjacent cells. Marginal cells 6-8μ l., 4-6μ br., coenobia 20-25μ diam.

2. Tetraedron planctonicum G. M. Smith (Text-fig. 1, 2).

This rather delicate *Tetraedron* species occurred in small numbers in the late summer plankton of the eutrophic Lindores Loch, Fife (37/265165). The cells, which are polyhedral-pyramidate with 4 or 5 angles, have distinctly convex sides while the angles are produced to form slender, more or less parallel-sided, furcate processes, each furca being tipped with 2, or more rarely 3, delicate, divergent spines. These plants seem to be more slender than the American forms of this species (Smith 1922, Prescott 1951) and were it not for the fact that the processes are distinctly branched, they could be referred to *T. hastatum* var. *palatinum* (Schmidle) Lemm. Cells 15μ diam. without processes; 30-40μ diam. with processes.



TEXT-FIG. 1.

1. PEDIASTRUM TETRAS var. TETRAODON (Corda) Rabenh.
2. TETRAEDRON PLANCTONICUM G. M. Smith
3. TETRAEDRON GRACILE Borge
4. TETRAEDRON ENORME (Ralfs) Hansg.
5. TETRAEDRON LUNULA (Reinsch) Wille
6. TETRAEDRON LUNULA (Reinsch) Wille
7. TETRAEDRON TRIGONUM var. GRACILE (Reinsch) De Toni
8. ANKISTRODESMUS ACICULARIS (A. Br.) Skuja

3. TETRAEDRON GRACILE Borge (Text-fig. 1, 3).

A much more robust form of this species than that previously described from Sutherland (Brook 1957), but still with the very characteristic twice branched angles of its cells all lying in the same plane but at an angle of 90° to one another, has been found in net hauls from Ridge Loch, Sutherland (29/335332). It differs from these previously described Scottish specimens in that the forked spines, with which the processes are tipped, are much stouter and not all lying in the same plane as the body of the cell.

4. TETRAEDRON ENORME (Ralfs) Hansg. (Text-fig. 1, 4).

Considerable numbers of this species, the angles of whose polyhedric cells are produced to form short bifurcate lobes terminating in pairs of stout spines, were present in small pools near Loch Bhac, Perthshire (27/822622). Cells up to 50μ br.

5. TETRAEDRON LUNULA (Reinsch) Wille (Text-figs. 1, 5, a-e; 1, 6).

This species, which does not seem to have been recorded before from Britain, has been found in considerable amounts in plankton hauls from Loch na Craige, Perthshire (27/883455) and Loch Spynie, Morayshire (38/257665) in June and July. The cells are typically lunate and taper to distinctive poles which may be blunt or quite sharply pointed. Their outer margins in side view are more sharply curved than the inner, which may in some cases (Text fig. 1, 5 a, c and d) have a marked depression in the centre. In face view (Text fig. 1, 5 b), the sides of the cells show more or less equal curvature. In the material from Loch na Craige the cells tended to remain in groups of four, each group, it is presumed, having developed from four autospores liberated from a single parent cell. Cells 25-30μ l., 5-8μ br.

6. TETRAEDRON TRIGONUM var. GRACILE (Reinsch) De Toni (Text-fig. 1, 7, a-c).

Occasional specimens of this variety, whose cells have very delicate cell walls and can thus be easily overlooked, especially in preserved material where the colour has faded from the chloroplasts, have been found in the plankton of Loch Calder, Caithness (39/670610). The cells are usually flat, the slender, considerably produced, tapering angles of which terminate in a sharp spine, all tend to lie in the same plane. In some specimens the

angles are markedly curved and the sides of the cells extremely concave (Text-fig. 1, 7 b). Diameter, including spines, 35-40μ.

7. ANKISTRODESMUS ACICULARIS (A. Br.) Skuja (Text-fig. 1, 8).

The solitary, fusiform cells of this species which may be straight, slightly curved or sigmoid, with their characteristic long and finely drawn-out apices, were common in the plankton of Loch na Beiste Brice, Sutherland (29/238501). The illustrations of this alga in West and Fritsch (1931, Fig. 40 B and C), where it is referred to as the var. *acicularis* (A. Br.) G. S. West of *Ankistrodesmus falcatus* (Corda) Ralfs, do not seem to represent it adequately, for the finely hair-like, attenuated, apices are not shown, and, in fact, there would seem to be little difference between these figures and those depicting the var. *mirabilis* W. & G. S. West (West and Fritsch *loc. cit.* Fig. 40D). The size of the Loch na Beiste Brice cells was very variable, ranging from 50μ l. and 2·5μ br. in the case of young cells, to 125μ l. and 4μ br. in old cells just before division.

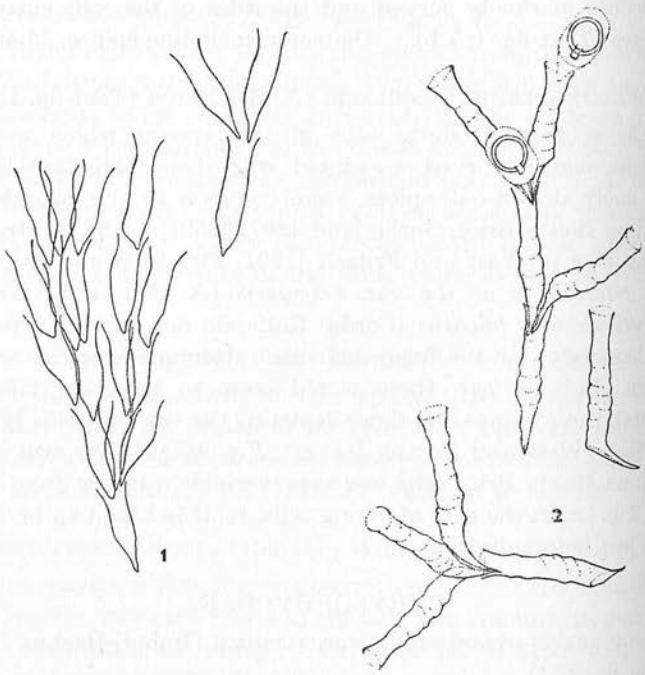
CHRYSOPHYCEAE.

1. DINOBRYON CYLINDRICUM var. ALPINUM (Imhof) Bachm. (Text-fig. 2, 1).

This variety, which seems to be intermediate in character between its type species and *D. sertularia* Ehr. and which has not been previously recorded from Scotland, was frequent in the spring plankton of the Ridge Loch, Sutherland. The envelopes, which vary in size from 45-55μ l. and 10-11·5μ br., are arranged in much more compact colonies than the type species.

2. DINOBRYON DIVERGENS var. SCHAUINSLANDII (Lemm.) Brun. (Text-fig. 2, 2).

This variety of *D. divergens* Imhof, is fairly widely distributed in the plankton of meso-oligotrophic Scottish lochs. Some particularly fine colonies have been found in a sample from Loch Meadie, Sutherland (29/402645) with unusually long, though typically undulate envelopes of up to 75μ l. Their breadth varied from 9-12·5μ. A considerable number of the envelopes bore cysts within characteristic membranes, 25μ l. and 20μ br., just outside the aperture of the envelope. The cysts themselves, which are spherical, were of larger size than those noted by Huber-Pestallozi (1941, p. 229), being 17·5μ in diameter.



TEXT-FIG. 2.

1. DINOBRYON CYLINDRICUM var. ALPINUM (Imhof) Bachm.
2. DINOBRYON DIVERGENS var. SCHAUINSLANDII (Lemm.) Brun.

CYANOPHYCEAE.

1. MARSONIELLA ELEGANS Lemm. (Text-fig. 3, 1).

This small blue-green alga, previously unrecorded from the British Isles, has been frequent at times in the early summer plankton of Loch Moraig, Perthshire. The colonies were usually of only 4 or 8 pyriform cells, sometimes slightly curved and radiately arranged with their broad ends directed inwards. These groups of cells are enclosed within a transparent mucilage envelope which usually can only be seen by staining or by mounting in Indian ink. Cells 2-2·5μ br., 6-7μ l. Colonies, without mucilage investment 15μ diam., with mucilage 25μ diam.

2. DACTYLOCOCCOPSIS ACICULARIS Lemm. (Text-fig. 3, 2).

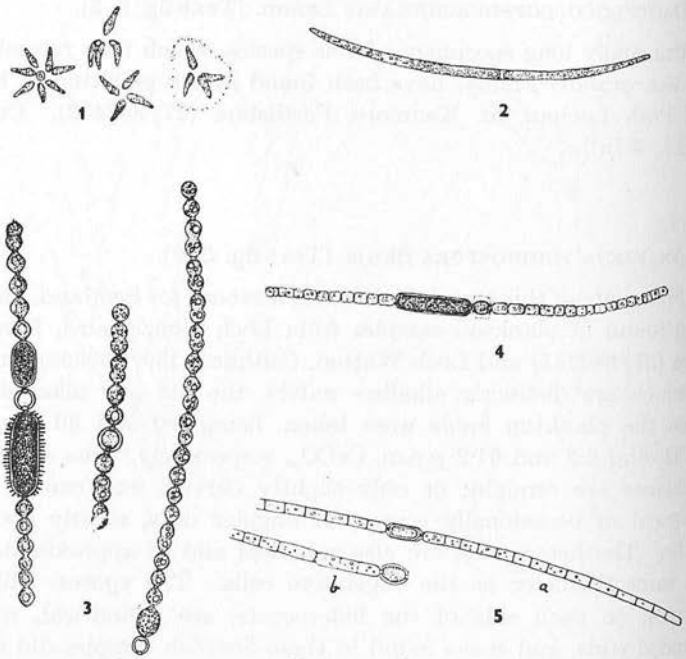
Unusually long specimens of this species, which thus resemble the var. *grandis* Fremy, have been found in the plankton of the Hill Park Lochan, nr. Kenmore, Perthshire (27/802432). Cells 160μ l., 3·7μ br.

3. ANABAENA ECHINOSPORA Skuja (Text-fig. 3, 3).

Filaments of this alga, which is a new record for Scotland, have been found in plankton samples from Loch Monzievaird, Perthshire (27/842233) and Loch Watten, Caithness (39/230560), both of which are distinctly alkaline waters, the pH and alkalinity, when the plankton hauls were taken, being 8·0 and 60 p.p.m. $CaCO_3$ and 9·3 and 61·2 p.p.m. $CaCO_3$, respectively. The solitary trichomes are straight, or only slightly curved, and consist of spherical or occasionally somewhat angular cells, mostly about 8μ br. The heterocysts are also spherical and of approximately the same diameter as the vegetative cells. The spores, which develop on each side of the heterocysts, are cylindrical, with rounded ends, and those found in these Scottish samples did not exceed 40μ l. and 13μ br. The spores when mature are decorated with a dense cover of short colourless spines (extruded mucilage?).

4. ANABAENA CYLINDRICA Lemm. (Text-fig. 3, 4).

A few trichomes of this blue green alga have been found from time to time in plankton samples from Loch na Beiste Brice. They are composed of series of cylindrical cells with broadly rounded ends, those at either end being smaller than the cells in the middle region of the trichome thus giving it a tapered appearance. The free end of each terminal cell is rounded. The broadest cells in the central region are never more than 5μ in width and up to 7·5μ long, while those at the ends taper to 3μ in breadth. The heterocysts are ovoid and of about the same dimensions as neighbouring cells, being 5μ br. and 7·5μ l. Each heterocyst is surrounded by a wide, colourless mucilage envelope, while the spores which develop adjacent to the heterocysts are cylindrical and slightly broader than the other parts of the trichome (usually 6-7μ) and up to 25μ l.



TEXT-FIG. 3.

1. MARSONIELLA ELEGANS Lemm.
2. DACTYLOCOCCOPSIS ACICULARIS Lemm.
3. ANABAENA ECHINOSPORA Skuja
4. ANABAENA CYLINDRICA Lemm.
5. ANABAENA SUBCYLINDRICA Borge

5. ANABAENA SUBCYLINDRICA Borge (Text-fig. 3, 5 a and b).

According to Geitler (1932) there is little reason to separate this species from the above mentioned *A. cylindrica*. Borge's figures (see Huber-Pestallozi 1938, Abb. 124), however, show distinct differences in the shape of the cells and heterocysts and in the character of the spores. Specimens of an *Anabaena* species which can only be referred to this species have been found in the plankton of the middle loch of the Lochan nan Ealachan group of lochs, Sutherland (29/328346). In these, the cells which form the straight, slightly tapering trichomes are distinctly rectangular, with only very slight constrictions between each cell. Their breadth varies between 4-5·5μ from the end to middle of each trichome and their length from 5-8μ. The heterocysts, which are

of about the same width as the vegetative cells, are surrounded by a narrow colourless envelope, their width and length being 6μ and 12μ respectively. Occasional trichomes have been observed (Text-fig. 3, 5 b) in which there are terminal heterocysts, oval in shape and thus differing radically from those which must be regarded as typical. No spores were observed.

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ON SOME FORMS OF *MICRASTERIAS* NEW TO OR RARE IN BRITAIN

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1. *Micrasterias truncata* (Corda) Bréb. var. *neodamensis* (A. Braun) Dick. *Krypt. Forsch. Bayer. Bot. Ges. München*, **7**, 448, 1926. (Fig. 1.)

Resembling the type species in size and general proportions, but differing in that the lateral lobes are divided only by a short incision to form a pair of lobules which bear short, stout teeth at each angle (the lower semi-cell in Fig. 1 is atypical in this respect). The incisions which separate off the polar lobes from the lower portions of each semi-cell are deep and usually closed, as in the type species, while the polar angles are strongly accuminate. Previously recorded from Wales (Woodhead and Tweed, 1954), a form which clearly resembles this variety is figured in West and West (1905), Pl. XLV, fig. 5. 70μ l., 65μ brd., 17μ at isthm.

Rare in plankton of Point Loch, Sutherland (Grid Ref. 29/301420).

2. *M. mahabuleshwarensis* Hobson var. *europea* Nordst. *K. Vet. Ak. Handl*, **22**, 31, 1888. (Fig. 2.)

The sinus dividing the basal lobes of the semi-cells is deep and open as is also the incision separating the individual lateral lobes thus forming long, tapering and usually spiny, undivided lobules. The incisions between the lateral lobes and polar lobes are wide, the latter being large and extended, the upper portion being produced laterally to form divergent, denticulate processes which are almost equal in length to the lateral lobules. In addition, the apex bears a pair of denticulate accessory processes asymmetrically disposed between the lateral processes. Two rows of stout apical verrucae, usually four in number, are situated between these processes. The middle of each semi-cell above the isthmus is swollen, forming a small protuberance and bearing two granules. The semi-cells bear more or less complete rows of intramarginal spines within the primary divisions of the cell. 180μ l., 140μ brd., 22μ at isthm.

Rare in the plankton of Loch an Daimh Mor, Sutherland (Grid Ref. 29/159432).

3. *M. mahabuleshwarensis* Hobson var. *dichomata* G. M. Smith. *Trans. Wisc. Acad. Sci. Arts and Letts.*, **20**, 345, 1922. (Fig. 3.)

As Krieger (1937) states, this variety is somewhat difficult to separate from certain forms of *M. americana*. However, the ornamentation in particular, of the present specimens seems to indicate an affinity with *M. mahabuleshwarensis*, each semi-cell in the middle above the isthmus being furnished with a small denticulate protuberance and with a distinct series of intramarginal granules along the primary divisions of the cell, these being especially distinct along the base of the lower lateral lobes. There are also a prominent pair of granules on each side of the base of the incision which divides the apical lobe from the lower part of the cell. Also typical of *M. mahabuleshwarensis* are the well defined apical verrucae, a feature with according to Teiling (private communication) is seldom lacking in this species. The arms of the lobules, however, which are 2-5 spinate at their extremities are shorter than those shown in the figures depicting the var. *dichotoma* in Krieger (1937) Taf. 110, fig. 4, or in Prescott and Scott (1952), Pl. VI, fig. 3, and thus resemble those of *M. americana*. 120μ l., 100μ brd., 25μ at isthm. Recorded from Wales by Woodhead and Tweed (1954).

Rare in the plankton of Bassenthwaite, Cumberland.

4. *M. mahabuleshwarensis* Hobson var. *Wallichii* (Grun.) West and West, *Brit. Desm.*, 2, 122, t. 54 figs. 7, 8; t. 55 figs. 1-3; 1905, forma *spinosa* fa. nov. (Fig. 4.)

A form of this quite commonly occurring variety in which a series of well-defined denticulations, increasing in size from apex to base and extending down the lateral margins of the apical lobes, was quite frequent in the summer plankton of Loch Shurrery, Caithness (Grid Ref. 39/044555) in 1950. The denticulations on the lateral lobules were also more strongly developed than normal.

5. *M. americana* (Ehr.) Ralfs *Brit. Desm.* xix, 1848, forma *reducta* fa. nov. (Fig. 5.)

A greatly simplified form of this species has been found in the plankton of Loch Eagheach, Perthshire (Grid Ref. 27/455568). In this form the accessory processes of the polar lobes are completely absent (cf. var. *Lewisiana* West), though the polar

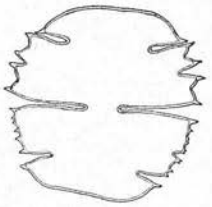

FIG. 1
M. truncata (Corda) Bréb. var. *neodamensis* (A. Braun) Dick.

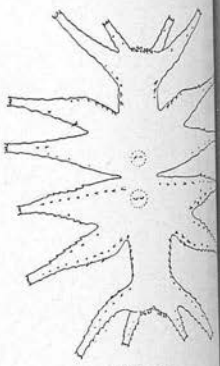

FIG. 2
M. mahabuleshwarensis Hobson *europea* Nordst.

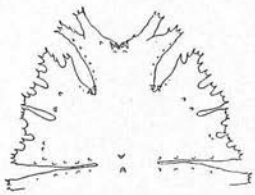

FIG. 3
M. mahabuleshwarensis Hobson var. *dichotoma* G. M. Smith.

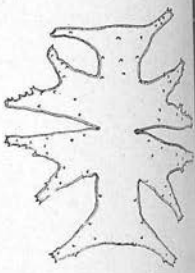

FIG. 5
M. americana (Ehr.) Ralfs *reducta* fa. nov.

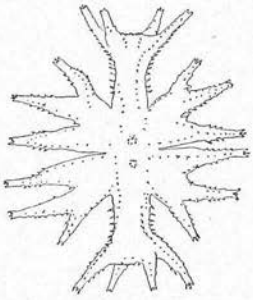

FIG. 4
M. mahabuleshwarensis Hobson var. *Wallichii* (Grun.) West and West forma *spinosa* fa. nov.

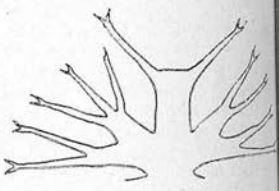

FIG. 6
M. radiata Hass. var. *dichotoma* (Wolle)

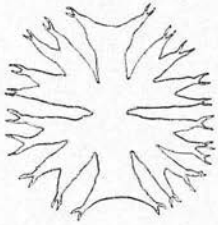

FIG. 7
M. radiata Hass. var. *pseudo-crux* Grönblad

FIG. 8
M. radiata Hass. var. *evoluta* Krieg.

The Natur

lobes themselves are no shorter than in the type species. The incisions between the lateral lobes are deep and the lobes widely divergent. There is no subdivision of the upper lobes, but the slightly longer lower lobes each bear a very small lobule halfway along the upper margin. Lobes tipped with one to four sharp teeth. A few scattered granules present on the surface of both polar and lateral lobes. 120μ l., 120μ brd., 22μ at isthm.

6. *M. radiata* Hass. var. *evoluta* Krieg. Rabenhorst's Kryptog. fl., **13** (2), 71, 1937. (Fig. 8.)

One specimen which can be referred to this variety, previously recorded from Wales (Woodhead and Tweed, 1954), has been found in the plankton of the Mill Dam, Kinnaird Estate, Perthshire (Grid Ref. 27/970496). It is distinguished by a pair of asymmetrically disposed accessory processes between the polar lobes similar those found, for example, in *M. americana*. A further unusual feature of this particular specimen is the arrangement of the upper pair of lateral lobules which are at right angles to one another, an aberration previously recorded by West and West (1905) Pl. LII, fig. 9. 140μ l., 130μ brd., 17μ at isthm.

7. *M. radiata* Hass. var. *pseudo-crux* Grönblad. *Acta. Soc. Flora Fauna fenn.*, **47**, 37, 1920. Fig. 7.)

In its general shape this variety may at times be confused with some forms of *M. crux melitensis* (Ehr.) Hass. and *M. radians* Turn. (See Prescott and Scott, 1952, Pl. VIII, fig. 4, and p. 247.) However, the open sinus and the shape and disposition of the polar and lateral lobes with their deeply furcate apices show its clear affinity with *M. radiata* (see Grönblad (1920) Taf. VI, figs. 12 and 13).

Rare in the plankton of Loch Chaluim, Caithness (Grid Ref. 39/022519). 110μ l., 105μ brd., 18μ isthm.

8. *M. radiata* Hass. var. *dichotoma* (Wolle) Cushm. *Rhodora*, **10**, 97, 1908. (Fig. 6.)

Occasional specimens with lateral lobules of considerable length (up to 60μ l.) and which can therefore be referred to this variety have been found in the plankton of Loch Eagheach. 180μ l., 170μ brd., 26μ isthm.

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15

THE STATUS OF DESMIDS IN THE PLANKTON AND THE DETERMINATION OF PHYTOPLANKTON QUOTIENTS

BY A. J. BROOK

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THE STATUS OF DESMIDS IN THE PLANKTON AND THE DETERMINATION OF PHYTOPLANKTON QUOTIENTS

By A. J. BROOK

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(*With six Figures in the Text*)

A comparatively recent aspect of botanical research in freshwaters has been concerned with attempts to relate the specific composition of the phytoplankton community to the trophic status of lakes. Based on the supposition that certain algal groups, such as Myxophyceae and Chlorococcales, are eutrophic in their preference in contrast to others, particularly Desmidieae, which are specifically most numerous in oligotrophic waters, a number of plankton quotients have been devised to express the degree of richness, or poverty of standing waters (Thunmark 1945, Nygaard 1949). In making these quotient determinations, net hauls of phytoplankton are examined and the number of species in the relevant groups present enumerated. In such collections, however, it is not uncommon to find, in addition to truly planktonic forms (euplankters), considerable numbers of adventitious forms from other habitats (tychoplankters). Since quotients are based entirely on the numbers of species present, irrespective of their abundance, it is clearly of considerable importance to discriminate between these true and chance plankters. This possible source of error applies particularly in the case of desmids which, as the denominator, play a significant role in the Compound Quotient of Nygaard (1949) which is the most widely used and reliable of these quotients. For example, the inclusion of a number of tychoplanktonic desmids in a quotient determination will produce a misleadingly low indication of trophic status. Unfortunately, the separation of true from chance plankters is not always easy, for we do not yet know sufficient about the biology of many desmid species to be completely confident about their normal habitats. In addition, the situation may be complicated by the fact that some species which are normally benthic may be able to survive and even reproduce in the plankton. These are referred to as facultative plankters.

There does not appear to exist anywhere in the literature an adequate list of well-recognized euplanktonic desmids and thus the principal aim of the present investigation has been to attempt to determine which species, varieties, or forms of desmids encountered in the British freshwater plankton may be considered as true plankters and thus can be included in quotient determinations.

The most abundant and varied collections of desmids are to be found in *Sphagnum* bogs and amongst the shoots and leaves of inundated plants in weedy ponds and ditches. A somewhat similar habitat to the latter and also qualitatively and quantitatively rich in desmids is to be found in the interstices of the submerged vegetation of larger bodies of water such as ponds and lakes. They may also be abundant in the felts of filamentous algae which may develop on and around these plants. Some of the desmids occupying such habitats would seem to be fairly

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closely bound (though very rarely attached) to the macrophytes with which they are associated, while a considerable number appear to lead an almost free-floating existence in the water surrounding the plants so that quite frequently they are washed into the open water of the lake in which they occur. In addition to these important desmid habitats there occurs in most lakes a community of desmids which appear to be adapted to a completely free-floating existence and thus are truly planktonic. Griffiths (1928) has proposed three terms to describe these major desmid habitats, using 'terraqueous' for the community in bogs, pondlets or ditches, 'benthoplanktonic' for that amongst the submerged plants of weedy lake shores, and 'limnoplanktonic' for the open-water community of larger bodies of water.

In collections of plankton from the open water of a lake taken with a bolting silk net it is, however, possible to find desmids typical of each of these three habitats and it seems that even those forms from terraqueous habitats can survive for considerable periods, though they probably do not reproduce, in open water. Indeed, it seems to be generally accepted that planktonic desmids have originated from, and are but ecological varieties of, terraqueous species from bogs surrounding the lake, or at least of benthoplanktonic species derived from the submerged weeds of the littoral zone (Wesenburg-Lund 1905, West & West 1909, Griffiths 1928). West & West (1909) suggest that the adaptation to the planktonic habitat is an evolutionary process which has taken a very long time, though Griffiths (1928), from the examination of the plankton of reservoirs of about 30 to 40 years of age, was of the opinion that truly planktonic desmids do not necessarily constitute an ancient algal flora but suggests that they may in certain cases have evolved remarkably rapidly from desmids in moist and boggy places which have become inundated. In view of the fact, which unfortunately does still not seem to be fully recognized, that desmids are extremely plastic organisms, it seems probable that this process may even take place annually, and indeed some evidence has been accumulated (Brook, unpublished data) to support this view. These observations suggest that several limnoplanktonic 'species' are only ecological forms of species from terraqueous or benthoplanktonic habitats, though often differing very considerably from them in such characters as body shape and process length, and showing a considerable reduction in ornamentation. Thus it seems certain that as knowledge of such relationships becomes more firmly established, the nomenclature of many forms, previously considered to be separate species will have to be revised. It would seem logical that they should be named merely as forms of the species from which they are found to be derived.

Of the 690 species and 450 varieties of British desmids described by West & West (1904-23), only fourteen species and twenty-nine varieties are considered by these authorities to be exclusively planktonic, while twenty-three species and eighteen varieties would seem to be regarded by them as more often found in the plankton than in other habitats (West & West 1909). Griffiths (1928), however, has questioned the validity of the Wests' list of exclusively planktonic species and has drawn up an interesting table, listing alongside the fourteen species which the Wests believe to have no connection with the weedy habitat, those terraqueous or benthic desmids which he considers to be closely allied to them. Whilst some of the relationships postulated by Griffiths are erroneous in the light of recent studies (Teiling 1948, Brook 1959), such as the supposed relationship between

Arthrodesmus crassus and *Staurastrum jaculiferum*, *S. affine* and *S. polymorphum*, *S. dorsidentiferum* and *S. gracile*, nevertheless, many of his objections to the Wests' list are cogent. Griffiths also objects to the Wests' list on the grounds that many of the species quoted are of very localized distribution. This, however, does not seem to be a reasonable objection, for since there is little evidence that planktonic desmids reproduce sexually (*i.e.* in many cases zygospores have never been recorded), such desmid populations must therefore be immense clones which have propagated themselves entirely by vegetative means over periods of possibly thousands of years. It is well known that the semicells of these plants are susceptible to considerable variation which may be the result of mutation or merely be a reflection of a change in environmental conditions. Any permanent mutation, in the absence of suitable means of dispersal, will, however, be confined and isolated within a given lake and be subjected to conditions comparable to those of a vast algal culture. Thus local races of a desmid ('formenkreis') with a very limited distribution may arise in a lake, or near-by group of lakes, and indeed it is known that several planktonic desmids have a very restricted distribution (*see* below). Thus the form of a given species from different lakes, even in a small area such as the British Isles, may show considerable variation (*see* Brook 1958c, Plates 1 and 2, 17 and 18) and in some cases, depending on the predilections of the investigator, these have been recorded as distinct forms or varieties or, in extreme cases even given specific rank. It seems that the environmental conditions existing in certain lakes (although what these conditions are is not known) seem to lead to the production of considerable variation. Thus in Lough Corrib in north-west Ireland one desmid sufficiently distinctive to be worthy of specific rank, *S. dorsidentiferum*, two very distinctive varieties of *S. furcigerum*, the var. *reductum* and var. *simplicissimum*, and a reduced form of *S. pelagicum* have been found in considerable numbers in its plankton (Brook 1958a).

It seems reasonable to assume that any desmid which occurs frequently in the plankton collected from the open water of large deep lakes must be considered to be truly adapted to this habitat, especially if a significant proportion of individuals of the species, variety or form in question are undergoing vegetative division. It then follows that the same taxa in the plankton of smaller, shallower lakes can also be considered as euplanktonic. On the basis of this assumption the desmid plankton from open-water net hauls collected in ninety-eight Scottish lochs for which accurate bathymetric data are available (Murray & Pullar 1910), has been carefully investigated and identified. As a result of this investigation Figs. 1 and 2 have been compiled in which is shown for each of the most frequently occurring desmid taxa, the range of the mean depth of the lochs in which they have been found. Where there is some obvious morphological relationship between the various taxa listed in Fig. 2, these have been grouped together. Such grouping tends to bring out the supposed evolutionary trend from benthic to planktonic forms, the latter in most cases occurring in much deeper lakes than the benthic forms from which they are considered to have been derived.

Each desmid genus, species, or variety which has been recorded in significant amounts in the plankton samples examined in this investigation will now be considered in detail. In certain cases, additional support for the conclusions reached has been provided by observations on the desmid plankton of a number of the English Lake District lakes and from lakes in other parts of the British

Isles. This is especially applicable in the case of certain eutrophic species, for the majority of Scottish lochs are of oligotrophic character.

Genus Closterium

There are only a few members of this large genus which would seem to be truly planktonic, most species being confined to terraqueous or benthic habitats. The most common of these in oligotrophic Scottish waters are *Closterium setaceum*, which has been found in open-water collections from a number of the deepest lochs and the closely related *C. kutzingii* which has been recorded from Loch Tay

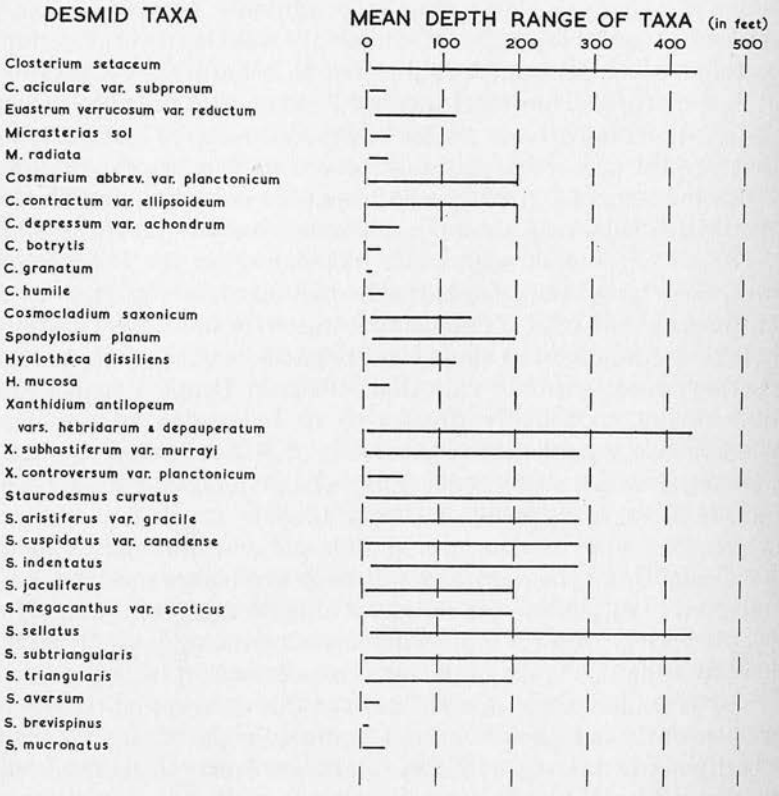

Fig. 1. Occurrence of desmids (genera other than *Staurastrum*) in the plankton of Scottish lochs in relation to their depth (1 ft = 0·305 m).

(508 ft (155 m) deep), Loch Achray (97 ft (29·6 m) deep) and Loch Doon (100 ft (30·5 m) deep).

Many species of *Closterium* would seem to have decidedly eutrophic tendencies and thus there is a possibility that the determination of true plankters on the basis of the depth of lake in which they occur will tend to overlook those few species which seem to be restricted in their occurrence in the plankton of shallow, eutrophic waters (shallowness itself is a morphometric character associated with eutrophy). Examples of this kind are *C. ceratium* and *C. pronum* which have been found in considerable abundance in shallow lakes in the Midlands of England; though from the Wests' observations on these species these would appear to

be merely facultative plankters. With reference to Scottish lochs which are the primary concern of the present investigation, it has been observed that *C. aciculare* var. *subpronum* occurs in abundance at times in the open-water plankton of a number of shallow lochs. Occasionally it has been found to be the only desmid present in some plankton collections. The absence of this species from the plankton

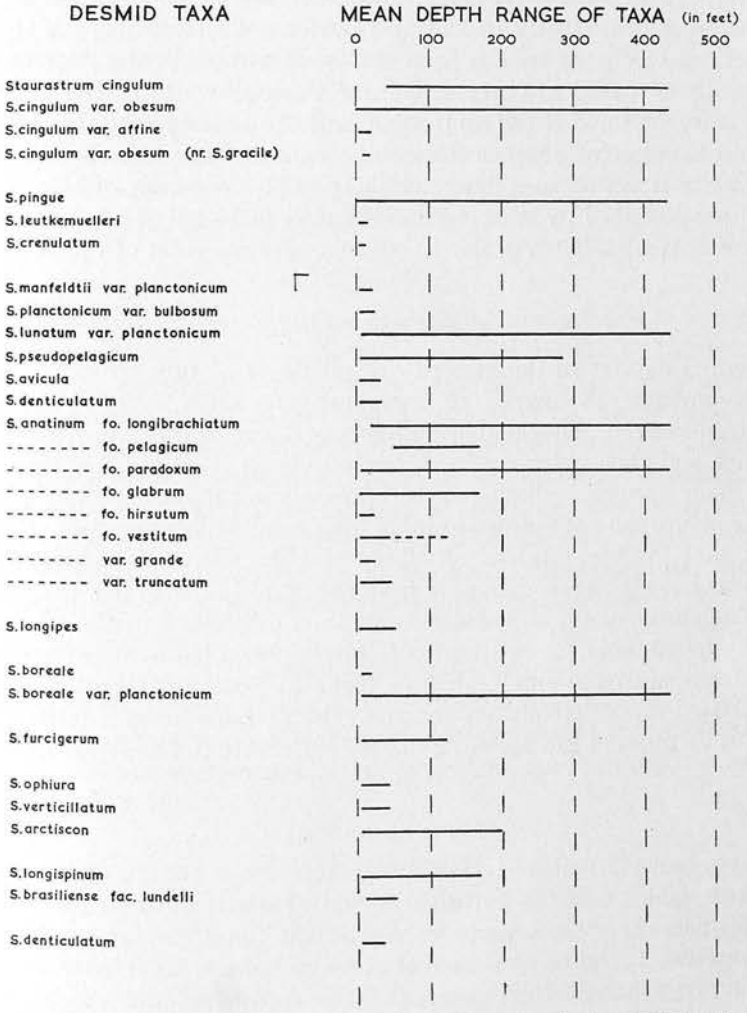

Fig. 2. Occurrence of desmids of the genus *Staurastrum* in the plankton of Scottish lochs in relation to their depth.

of deeper lakes would seem to be a reflection of the fact that it is limited in its distribution to relatively alkaline lakes (alkalinity above 20 p.p.m. $CaCO_3$) of which there are no deep ones in Scotland. Although it occurs in abundance in waters which are fairly eutrophic (*e.g.* Loch Leven) it is also present in the plankton of highly calcareous marl lakes (alkalinity over 100 p.p.m.) in which plankton production is usually extremely poor (*e.g.* the Durness Lochs, Sutherland).

Genus Euastrum

Although a considerable number of species and varieties of this genus hav been found in the plankton collections from the shallower lochs investigated durin the present study, they have only been occasional individuals. They are almo certainly all tychoplankters since the normal habitat of members of this genus i in bogs or amongst the weeds of the margins of large reedy ponds and lakes. Ther is, however, one notable exception in *Euastrum verrucosum* var. *reductum* whic has been found consistently in the open-water collections from a considerabl number of deep lochs, as well as from shallower waters, in the west of Scotland It has also been found in the plankton of Bassenthwaite in the English Lak District (max. depth 75 ft (23 m)). Although the type species also occurs in th plankton it is doubtful whether this can be regarded as more than a facultativ plankter since it occurs in abundance in the littoral region of lakes. The va *planctonicum* described by West & West from the plankton of two lochs in Suther land (West & West 1903) is probably only an extreme form of the var. *reductum*

Genus Micrasterias

The normal habitat of the majority of members of this genus is in bogs an especially amongst the weeds of comparatively small, shallow lakes. Quit frequently, however, considerable numbers of these plants are carried into th open water and thus occur in plankton collections, though it is most doubtfu whether many species, including such commonly occurring forms as *Micrasterias sol* or *M. radiata*, can be regarded as more than facultative plankters. It is possible however, that the var. *murrayi* of *M. sol* and the var. *dichotoma* of *M. radiata* which so far have been recorded only from the plankton, may in fact be planktonic forms. The status of *M. mahabuleshwarensis* f. *wallichii* and the var. *europea* i probably euplanktonic, for in addition to having been found only in the plankto of a few comparatively small, shallow lochs in Scotland (West & West 1905 Brook 1957), Pearsall (1932) has recorded the f. *wallichii* as a fairly significant component at times of the plankton of Bassenthwaite (max. depth 75 ft. (23 m)

Genus Cosmarium

This large genus is almost exclusively terraqueous or benthic in habit but there are two taxa which occur in British freshwaters which must be regarded as true plankters. These are *Cosmarium abbreviatum* var. *planctonicum*, and *C. depressum* var. *achondrum*. It can be seen from the analysis of the occurrence of these taxa in relation to depth in Scottish waters that this desmid is limited to comparatively shallow lochs. This is undoubtedly on account of its more frequent occurrence in eutrophic waters, for it does occur, sometimes in abundance, in the plankton of a number of the deeper English lakes which are considerably more eutrophic than any of comparable depth in Scotland. It is common, for example, in Windermere (max. depth 219 ft (66 m)) and also occurs in Ullswater (max. depth 205 ft (62 m)).

Other *Cosmarium* species which are found quite frequently in plankton collections are *C. botrytis*, *C. contractum* var. *ellipsoidium*, *C. humile*, *C. impressulum*, *C. moniliforme* and *C. granatum*, the latter species especially in eutrophic waters. However, it is doubtful whether any of these species can be considered as more

than facultative plankters since they have been recorded so frequently from benthic habitats (West & West 1908, 1911).

Genus Cosmocladium

The only species of this genus, which contains the truly colonial, as distinct from the filamentous forms, of Cosmariae, to be found in the plankton is *Cosmocladium saxonicum*. It has been found in considerable amounts in the open water of some of the deeper Scottish lochs as well as in the plankton of Crummock Water, Windermere and Loweswater which are amongst the deepest of the English lakes. West & Carter (1923) also record it from the plankton of Welsh and Irish lakes. Since, however, it also occurs in bogs it is probably only a facultative plankter, though occasionally a very successful one, for Lund (private communication) has recorded a population of over 1000 cells per millilitre from Esthwaite Water, a fairly eutrophic lake in the English Lake District.

Genus Spondylosum

With the exception of *Spondylosum planum*, all the species of this genus of filamentous desmids would seem to be terraqueous or benthic in habitat, though *S. papillosum* has been found on occasions and often in quantity in plankton samples from shallow lakes. *S. planum*, however, is frequently an important constituent of the plankton of a number of the largest and deepest Scottish lochs. It is also quite common at times in the plankton of twelve out of fourteen of the largest of the English Lake District lakes which have been examined. It is suggested that the filamentous habit and mucilage-secreting propensities of this species and of the planktonic species of the genus *Hyalotheca* (*see* below) are characters which have contributed to their success as plankters.

Genus Hyalotheca

Two species of this genus, *Hyalotheca dissiliens* and *H. mucosa* are frequently encountered in considerable abundance in plankton collections, but since both are known to thrive in terraqueous habitats it seems that they can only be considered as facultative plankters.

Genus Xanthidium

The only planktonic members of the genus *Xanthidium* belong to the *antilopeum* section which, as pointed out by several recent workers (Britt-Florin 1957, Teiling 1957) is in need of drastic revision. Of this group *X. antilopeum* var. *hebridarum* and the var. *depauperatum* are together the most frequently occurring taxa in the plankton of Scottish lochs of all depths. *X. subhastiferum* var. *murrayi*, and the facies *triquetra* which is common at times in the deepest basin of Loch Lomond (max. depth 623 ft (190 m)) are also euplankters (these also belong to the *antilopeum* section of the genus and should be renamed).

Also found only in the plankton is *X. controversum* var. *planctonicum* which would seem to be a local race of *X. antilopeum* of very limited distribution, being confined to the north-west of Sutherland and lochs in the Hebrides. It is, however, fairly common in the plankton in the deepest loch in this region, Loch Shin (max. depth 162 ft (49 m)) and is thus probably euplanktonic.

From evidence accumulated during this plankton study it is believed that t type species *X. antilopeum* is not a true constituent of the plankton, its norm habitat being the benthoplankton of the littoral region. Moreover, such spec as *X. armatum* and *X. cristatum* and their respective varieties which may occ from time to time in plankton collections, especially from small shallow lak should also be regarded as benthoplanktonic.

Genus Staurodesmus

Although a considerable number of the members of this genus, recently esta lished from sections of the genera *Arthrodesmus* and *Staurastrum* (Teiling 194 are benthic in their habitat, there would appear to be nine well-defined taxa whi are clearly truly planktonic (*see* Fig. 1). From the results of the present obser tions there is some doubt as to whether the three species *Staurodesmus aversu S. brevispinus* and *S. mucronatus* can be regarded as truly planktonic form However, the Wests (1903, 1905) have recorded *S. aversum* from the plankton two fairly deep Scottish lochs, Loch Sheil (max. depth 420 ft (128 m)) and Lo Shin (max. depth 162 ft (49 m)) whilst it has also been found (personal obser tions) in samples from Crummock Water (132 ft (40 m)) in the English lak *S. brevispinum* is also recorded from Loch Sheil and the form *major* from Thirlme and Ullswater. Thus it would seem that these two species may at least be regard as facultative plankters. With regard to *S. mucronatus* there is no comparab evidence to warrant its inclusion amongst the planktonic members of the genu though the var. *subtriangularis* of this species would appear to be a member this community. It has been found in quantity in the plankton of Thirlmere an Crummock Water (personal observations) and West & West (1903) record it fro Loch Doon (max. depth 100 ft (30·5 m)) as well as from the plankton of a numb of Welsh lakes.

Genus Staurastrum

The radiate species of this diverse and very artificial desmid genus are the mo numerous of the planktonic desmids in British waters both with regard to numbe of taxa present as well as quantitatively. It is in the members of this genu especially that it is possible to perceive the probable evolution of the planktoni forms from terraqueous or benthic species. The various species and species-group will now be considered in turn:

(i) Staurastrum gracile-cingulum *group*

The identity of *S. gracile* has recently been established from type material i the Jenner Herbarium of the British Museum (Brook, in press) and it has be shown in contrast to the widely accepted belief (*e.g.* Smith 1924, Lind & Pearsa 1945, etc. etc.) that it is probably a benthic desmid. However, forms close to th species but differing in the possession of divergent processes and more angula bodies than the type have been found in the plankton of six comparatively shallo eutrophic lochs. These are recorded in Fig. 2 as *S. cingulum* var. *obesum* nea *S. gracile*. The more common, tumid form of *S. cingulum* var. *obesum* occu throughout the trophic range and in lakes of all depths, though it appears to b most abundant in those of mesotrophic status. The var. *affine* is probably a loca race of the var. *obesum* and seems to be confined in its distribution to Caithnes

the Orkneys and Shetlands. The comparatively slender-bodied species *S. cingulum* with its long divergent processes has been found only in the open-water plankton of the deepest lochs and would therefore seem to be the best adapted taxon of this group to the planktonic habitat. From these forms it is possible to propose an interesting evolutionary sequence derived from the benthic *S. gracile* (*see* Fig. 3). This is clearly one of the cases mentioned earlier (*see* p. 430) in which the taxonomy should probably be revised and *S. cingulum* and its varieties renamed as forms or varieties of *S. gracile*.

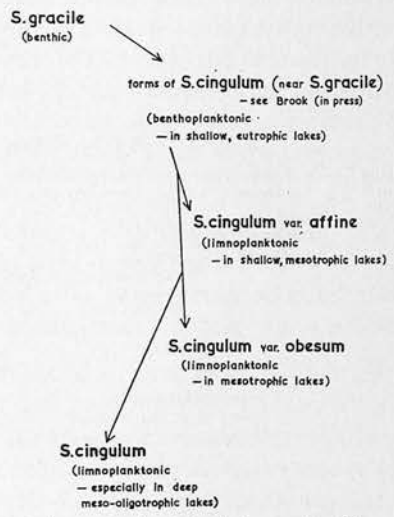

Fig. 3. Probable interrelationships between benthic and planktonic taxa of the *Staurastrum gracile* group of desmids.

(ii) S. proboscidium-boreale *group*

This *Staurastrum* group is closely allied to the *gracile-cingulum* group but differs principally in the disposition of the apical and sub-apical ornamentation of the semicell body (Brook, 1959). Both *S. proboscidium* and *S. boreale* are benthic desmids, though the latter has been found on occasions in the plankton of shallow weedy lochs of the Orkneys and Shetlands. Forms of *S. boreale* with very short processes have been found only in collections from the littoral in contrast to forms which would appear to be adapted to a planktonic existence, having long slender processes, have been found in the open-water plankton of a few Scottish lochs, including the very deep Loch Ness. These forms have been named *S. boreale* var. *planctonicum* (Brook 1959). Possibly related to this group, on the basis of its ornamentation (though clearly intermediate, connecting forms have not so far been discovered), is the long and very slender-armed *S. chaetoceras*. This species is markedly eutrophic in its tendencies and has been found to date only in one Scottish loch, the shallow, eutrophic Loch Leven. However, it occurs in Windermere, which is undoubtedly the most eutrophic deep lake in Britain, is common in Esthwaite Water and also occurs in a number of shallow, eutrophic reservoirs in the Midlands of England (*e.g.* Eyebrook Reservoir, Leicestershire, Swithland

Reservoir, Northamptonshire). Despite its frequent occurrence in shallow lak would nevertheless seem to be a truly planktonic species.

(iii) S. avicula-pseudopelagicum *group*

S. pseudopelagicum has been found in the plankton of sixteen of the lo examined, including some of the deepest. The most slender-bodied forms with longest processes have been found in the deepest lochs, whilst the more tu forms with shorter processes seem to occur in the shallower waters. These la forms approach *S. subcruciatum* in shape and this species in turn seems to h been derived from *S. avicula* through *S. arcuatum* (Brook 1957). These la species have been found only on rare occasions in open-water plankton collecti though they may be quite frequent in the shallows of weedy lakes. The suppo interrelationships within this species group are set out in Fig. 4.

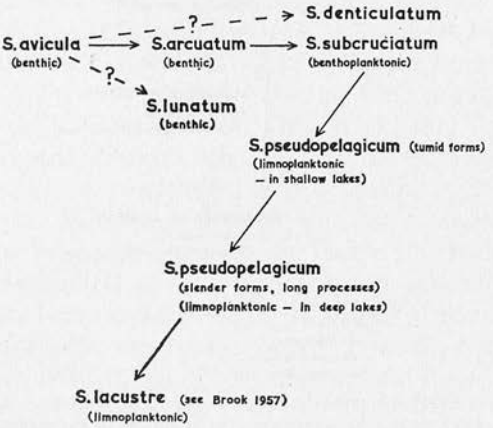

Fig. 4. Probable interrelationships between benthic and planktonic taxa of the *Staurastrum avicula* group of desmids.

The distinctions between *S. avicula* and some of the forms of *S. denticulatum* a *S. lunatum* are by no means clear and the taxonomy and interrelations of t species group require investigation. However, the forms of *S. denticulatum* wh are clearly distinguishable from *S. avicula* in possessing little or no discerni ornamentation on the body (a character associated with planktonic desmids, p. 439), have been found in moderate abundance in the plankton of some of t smaller, shallower lochs investigated but in none of the deeper ones. Thus it sho probably be regarded as a benthoplanktonic species, though the Wests (1909) ha recorded it from the plankton of the deepest of the English lakes, Westwa (258 ft (79 m)) and the moderately deep Ennerdale (148 ft (45 m)). It has a been found in Bassenthwaite, Loweswater, Coniston and Windermere (perso observations). Smith (1924), however, regards *S. denticulatum* as only a facultat plankter.

With reference to *S. lunatum* and the var. *planctonicum*, the type spe would seem to be associated with the benthic habitat, for its occurrence in plank samples is very sporadic and is mostly found in collections made in the littora shallow, weedy lochs. It is clear, however, from observations on the occurre of the very distinctive var. *planctonicum* that this taxon is limnoplanktonic, ha

been found in considerable abundance in the open water of the majority of the deepest lochs investigated. It also occurs in the plankton of the deepest English lakes.

(iv) S. anatinum *group*

The taxonomy of this very variable group has recently been considerably revised in an attempt to accommodate the multiplicity of forms which can be encountered. Some of these, despite their great variability, have been considered worthy of varietal rank by earlier investigators. It has been found, however, that very frequently two or more of the characters which previously have been considered to be so distinctive, may occur together in one plant which is then of course named according to the personal predilections of the investigator. In an attempt to eradicate this state of affairs, a number of character forms and a tri- or quadri-nomial nomenclature has been proposed (Brook, 1959). Of these character forms only the following would appear to be consistently associated with the planktonic habitat:

a. *longibrachiatum* = forms with long processes.
b. *pelagicum* = forms with elongated bodies.
c. *paradoxum* = forms with body ornamentation greatly reduced or absent.
d. *glabrum* = forms with ornamentation of the processes greatly reduced.

In many of the individuals of *S. anatinum* found in the plankton two or more of these characters are present together. The characters '*denticulatum*' and '*vestitum*' (*see* Brook, 1959) also occur in planktonic forms but not exclusively, since many benthic forms of the species also exhibit these characters.

The type species is without doubt a benthic alga as are also *S. anatinum* var. *grande* and the var. *truncatum* which occur quite frequently in the littoral plankton and amongst the weeds of small oligotrophic lakes.

This analysis in fact confirms the suggestion of Teiling (1947) concerning the general trends in planktonic evolution from benthic ancestors, the adaptation to the former (planktonic) habitat favouring a reduction in protuberances and ornamentation on the same cell body, the truly pelagic forms having the smoothest and least elaborate outlines. Thus the forms of the *anatinum* group best fitted to planktonic conditions are those with the characters *glabrum* and *paradoxum*. It is significant that these occur most frequently in open-water plankton collections from the deepest lochs.

(v) S. sebaldi-manfeldtii *group*

The interrelationships of this group are extremely complex and although broadly outlined by Teiling (1947) there are still several puzzling ramifications which require elucidation. In the first instance there seems to be some doubt about the validity of the relationship between Teiling's *S. sebaldi* var. *ornatum* f. *planctonicum*, *S. planctonicum* and its varieties, *S. sebaldi* itself. There is strong evidence to suggest that these forms are not in fact derived from *S. sebaldi* but instead from *S. manfeldtii* (Brook, unpublished data), and it is therefore believed that the name originally given to those forms which Teiling renamed *S. sebaldi* var. *ornatum* f. *planctonicum* should be retained: that is *S. manfeldtii* var. *planctonicum*. Considerable evidence has been gathered from plankton collections to

indicate that this variety, and also *S. planctonicum* which is often difficult separate from it, differing largely in the degree of reduction of ornamentation the semicells, are the planktonic derivatives of *S. manfeldtii*. These plankto forms exhibit a decided increase in length of body and processes over the ty species. Another planktonic derivative of *S. manfeldtii* is the var. *annulat* whose body again is much longer than in the type species. It is tentativ suggested that *S. longiradiatum* is closely related to this variety and as shown Fig. 5 where the probable interrelationships of this species group are shown, th are probably connections with *S. planctonicum* var. *bulbosum*.

Teiling has suggested a close relationship between the planktonic forms of *sebaldi-manfeldtii* group and *S. pingue*. This, however, seems open to questi and cannot be a very close relationship. On the other hand, it seems more reas able to suggest that *S. pingue* is in fact a planktonic derivative of the benthic *crenulatum*, with *S. uniseriatum* Nygaard as a connecting link (Brook, 19

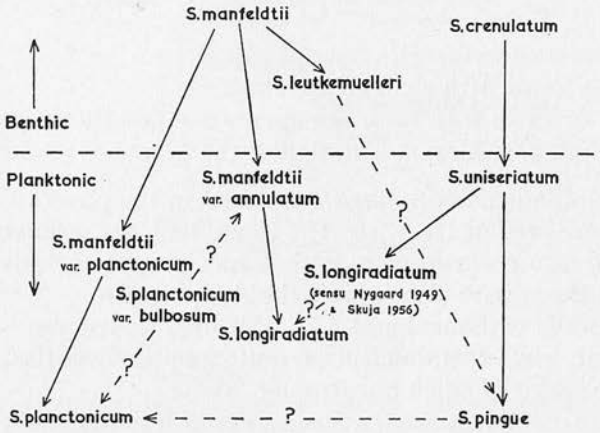

Fig. 5. Probable interrelationships between benthic and planktonic taxa of the *Staurastrum manfeldtii* group of desmids.

Plate 18, and in preparation). Here too the elongation of the body and proces in relation to the adoption of the planktonic existence mentioned above can b observed.

(vi) S. longipes

It is not possible to suggest which are the benthic relatives of this clear planktonic species, for although it was originally named as a variety of *paradoxum*, recent investigations have shown that this latter species has be increasingly used as a taxonomic dumping ground for a considerable number radiate *Staurastrum* species lacking distinctive body ornament and its abando ment has been proposed (Brook, in press). *S. longipes* is possibly related to th benthic *S. subgracillimum* through the var. *contractum* of the former. The latt has been found only in the plankton of comparatively shallow lochs in Scotla in contrast to the species which has been found in a number of deep lochs. Ev the type species, however, would seem to attain its greatest development in th plankton of fairly shallow, moderately eutrophic lakes (*e.g.* Lough Earne, Ireland

(vii) S. armigerum (*Breb.*) *Teiling* (= S. furcigerum *Breb.*)

The nomenclature of the *furcigerum* series of the genus *Staurastrum* has been revised recently by Teiling (1957) on the very logical basis that the primitive form should be the starting point of specific taxonomy and thus of nomenclature. Hence he suggests the revision of the group in a manner which would seem to accord with the theory that the planktonic forms have evolved from benthic ancestors. The supposed relationships between the various forms are shown in Fig. 6.

The var. *furcigerum* has been found in the plankton of waters of considerable depths along with other euplankton species. The fa. *reductum* and the var. *simplicissimum* are local varieties limited, as far as is known, to lakes in the west of Ireland.

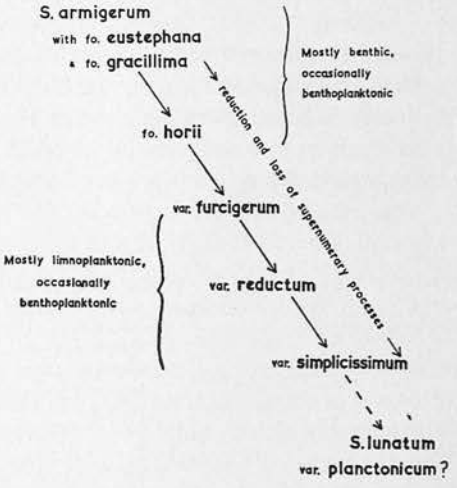

Fig. 6. Probable interrelationships between the benthic and planktonic taxa of the *Staurastrum armigerum* group of desmids.

(viii) S. longispinum

Although most abundant in the plankton of shallow lochs, this species has also been found, though never in quantity, in some of the deepest waters investigated. In these latter waters the paired spines with which the angles of the semicells are armed were often of considerable length (Brook 1958b). On the whole it seems to be a somewhat doubtful case, though the fact that West & Carter (1923) have regarded it primarily as a planktonic species found rarely in other habitats is additional evidence for considering it to be euplanktonic.

(ix) S. brasiliense *and the facies* lundellii

There is some doubt about the status of this species, for although found in some of the deepest of the English lakes it has been found only in comparatively shallow Scottish lochs and in greater abundance in the littoral. Thus it may only be a facultative plankter.

(x) S. ophiura *group*

Though occasional individuals of *S. ophiura* and *S. verticillatum* have be found in the plankton of quite a number of lochs, including some of the deep ones investigated (*see also* West & Carter 1923, p. 154), these two closely relat species are so essentially terraqueous in habitat, being most frequently found permanent *Sphagnum* bogs, that they can only be classed as tychoplankters.

(xi) S. arctiscon

This species has been found only in the plankton of the shallower lochs inves gated and thus it is believed to be benthoplanktonic. West & Carter (192 however, seem to regard it essentially as a planktonic species and have record it from a number of deep Scottish lochs and deep lakes in the English Lake Distric

Discussion

As a result of the analysis of the desmid populations in the plankton of a con siderable number of Scottish lochs and using the criterion that limnoplanktoni forms are rarely, if ever, found in habitats other than in the plankton and that significant number of individuals have been found undergoing division in the ope water of the deepest lochs, the following taxa would appear to belong to thi category:

Closterium setaceum
Cosmarium abbreviatum var. planctonicum
Micrasterias mahabuleshwarensis f. wallichii
Staurodesmus aristiferus var. gracile
S. curvatus
S. cuspidatus var. canadense
S. identatus
S. jaculiferus
S. megacanthus var. scoticus
S. sellatus
S. subtriangularis
S. triangularis
Euastrum verrucosum var. reductum
Spondylosum planum
Xanthidium antilopeum var. hebridarum-depauperatum
X. subhastiferum var. murrayi
Staurastrum cingulum
S. cingulum var. obesum
S. cingulum var. affine
S. boreale var. planctonicum
S. pingue
S. pseudopelagicum
S. lunatum var. planctonicum
S. anatinum f. longibrachiatum
f. pelagicum
f. paradoxum
f. glabrum
S. longipes
S. furcigerum var. armigerum
S. longispinum

Other essentially limnoplanktonic taxa are *S. manfeldtii* var. *planctonicum* and *S. planctonicum*, but because these are desmids having eutrophic tendencies they occur in Scotland only in comparatively shallow lochs for there are no deep, even moderately eutrophic waters in Scotland. However, confirmation of their euplanktonic character has been provided by their occurrence in the open water of some of the deep, comparatively rich lakes (*e.g.* Windermere) of the English Lake District.

Closterium aciculare var. *subpronum* is also a limnoplanktonic taxon, though it is also a special case in that it shows a decided preference for waters which are markedly alkaline and all of which in the British Isles are comparatively shallow. However, *C. aciculare* var. *subpronum* occurs in a large proportion of these and often it may be the only planktonic desmid present in waters of this type.

A considerable number of species found in the plankton have been classified as facultative plankters. These, although normally found in other habitats, can occur

in significant amounts and are known to be capable of multiplying in open water. Taxa included in this category are:

Micrasterias sol
M. radiata

Cosmocladium saxonicum
C. contractum var. ellipsoideum
C. depressum var. achondrum

Hyalotheca dissiliens
H. mucosa

Staurodesmus aversum
S. brevispinum

Forms of Staurastrum cingulum near
S. gracile
S. denticulatum
S. ophiura
S. verticillatum
S. arctiscon
S. brasiliense fac. lundellii

It is quite conceivable that further research into the origins of the desmid plankton may show that no clear distinction can be made between the two categories of desmids which have been separated in the lists given above. Even now there is some evidence to suggest that many limnoplankters are merely modified forms of terraqueous or benthic taxa (*see* above). In fact it may be that the principal distinction between limnoplankters and facultative plankters is that the form of those desmids in the latter category show no significant morphological changes when they occur in the plankton while those considered as limnoplanktonic do. The crux of this problem seems to be comparable with that which has already been posed in relation to a number of planktonic diatoms, *i.e.* how do these organisms over-winter? Do they fall to the bottom and remain dormant there until carried into circulation again in the following spring or early summer? Do a few individuals survive in the plankton throughout the winter (certain species have been found in collections taken in mid-winter in a number of lakes) and from these do the populations of the following summer develop? Or are most of the taxa derived from terraqueous or benthoplanktonic forms carried into the open water, where, if conditions are suitable, they reproduce and in certain cases undergo profound morphological change in this new habitat so that they are then considered to be separate species or varieties thought to be exclusively limnoplanktonic? As far as can be ascertained no investigation comparable with the researches of Lund (1949, 1954) or Knudson (1953, 1954) has yet been undertaken to elucidate these points for any desmid. Clearly research on this topic would be a most valuable contribution to our knowledge of desmid biology.

Finally, with regard to those forms which are regarded as tychoplanktonic (a term which could strictly be applied to all terraqueous and benthoplanktonic species), these usually occur only sporadically in the open-water plankton, as their name implies. Here their fate is probably to sink to the bottom as they die off because conditions are unsuitable for their existence. However, it must be borne in mind that even for desmids which are accepted as belonging to this category, conditions in the open water of a certain lake may for a time favour their growth and reproduction and then clearly they must be regarded as facultative plankters. Thus the distinction between these two categories of desmids, as in the case of limnoplankters and facultative plankters, is by no means well defined (*see* case of *Cosmocladium saxonicum*, p. 435). Indeed, even those taxa which at present seem to be fairly well established as limnoplanktonic may yet be shown to be merely ecological forms of taxa from other habitats.

Clearly the uncertainty and lack of precise distinction between the habitats of desmids apparent from the foregoing analysis, seems to impose a quite serious

limitation on the value of phytoplankton quotients, for in most of these the numb of desmid species present is used as the denominator. Thus the question arises to whether only those taxa thought to be exclusively planktonic (limnoplankt should be included; or are those facultative plankters which are found to present in some abundance and are reproducing in the open water also to be us thus introducing a quantitative factor into the determination which adds seve complications? On the other hand, if all desmids present in the sample a included, this will tend to weight the result obtained towards oligotrophy, p sumably in direct proportion to the size and degree of weediness of the la sampled: *i.e.* the smaller, shallower and weedier the lake, the greater will be t chance of large numbers of tychoplanktonic desmids being present. These co siderations thus introduce a note of vagueness and lack of precision into t quotient concept, for unless it can be stated with some certainty which desm are to be included, and which omitted from determinations (and this can be do only vaguely at present), the results of any assessment of trophic status on t basis will depend too much on the predilections of the investigator. This co sideration also applies of course to other groups of algae. In addition, the lim of species, even for the desmid specialist, are often difficult to define, especially the case of the genus *Staurastrum*, the taxonomy of which shows considera confusion owing to two opposing tendencies. These are that on the one hand t much attention is paid to minor details of shape and ornamentation with the res that many species have been founded on very variable and imperfectly studi characters, while on the other, many good species possessing only one comm character have all been referred to one ill-defined species. The most striking ca of this is *S. paradoxum* (*see* Brook, 1959 and Brook, in press). These co siderations alone make it very evident that quotient determinations of one inves gator may not be at all comparable with those of another.

These clearly add considerable weight to the suggestion of Nygaard (1949, p that the quotients devised by himself and Thunmark must only be considered provisional. The final aim, it seems, must be the formulation of a quotient bas only on a limited number of plankton species whose status in the plankton a whose trophic requirements have been found to be well defined; that is, clear limnoplanktonic species which are distinctly oligo- or eutrophic.

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4.

THE PHYTOPLANKTON OF SOME IRISH LOUGHS AND AN ASSESSMENT OF THEIR TROPHIC STATUS.

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INTRODUCTION.

DURING early September 1953 one of us (F. E. R.) collected phytoplankton with a net (180 meshes/inch) from the margins of 26 loughs in counties Clare, Galway, Mayo, Sligo, Roscommon, Leitrim and Fermanagh (Table VIII). Some were alkaline with shore deposits of calcified material and others acidic with peat deposits and *Eriocaulon-Lobelia* vegetation. No quantitative estimations were made, but the abundance of the commoner species is indicated in Tables I and II.

The data presented are based on single samples of littoral plankton. However, on the loughs, it is unlikely that this differs markedly from that in the central regions. Every effort was made to avoid contamination with benthic algae. Nygaard (1949) has shown that single samples taken in summer can be used to determine phytoplankton quotients (see p. 177). Though the dominant forms are unlikely to be the same at other times of the year, one of us (A. J. B., unpublished data) has found that the specific composition of the phytoplankton, and hence its quotient, varies little throughout the year, or from one year to another.

GENERAL FEATURES OF THE LOUGHS.

The following lie in basins composed largely or wholly of Carboniferous Limestone, and receive most of their inflow from the same formation or from drift deposits derived from it : Glencar, Colgagh, Conn, Arrow, Rea, Bunny. The same is true of the two turloughs, Tirneevin and Caherglassan. The basins of Loughs Erne, Carrick, Melvin, Gara, Corrib (which was sampled at two stations; in the north near Cornamona and the south near Gortmore) lie partly and Key and Cullin wholly on acid rocks (granite, quartzite, sandstone or shale), but receive most of their inflow from limestone

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TABLE. I.—*The phytoplankton exclusive of Desmids.*

	Key	Gill	Bunny	Rea	Arrow	Colgagh	Erne	Carrick	Cullin	Caherglassan	Talt	Glencar	Conn	Melvin	Tirneevin	Gara	Levally	Corrib (N.)	Corrib (S.)	Beltra	Aunierin	Derrygclare	Arddarry	Bofin	Oorid	Ballynahinch	Kylemore
Melosira varians, C. A. Ag.	..	+			+	+	+	+		+		+		+													
M. granulata (Ehr.), Ralfs.	..		+	C	+	+	C	+	+		+		+	+	+												
M. italica subarctica, O. Müll.	..	+			+	+	+	C		C	+		+	+	+												
Cyclotella comta (Ehr.), Kütz.	..				+			+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
Stephanodiscus astraea (Ehr.), Grun. ...		+	+		+		+	+		+		+	+	+		+										
Tabellaria flocculosa var. *flocculosa* (Roth.), Knud. ...																											
T. flocculosa var. *asterionelloides* (Grun.), Knud. ...		O	+		O	+	+	C		+		O	O	+		C	+	O	C	C		F	C	O	C	O	
T. flocculosa var. *pelagica*, Holmboe ...														+													
T. flocculosa var. *tetlingii*, Knud. ...									+	+				+													
T. fenestrata (Lyngb.), Kütz. ...						+	+				+			+		+	+	+	+								
Diatoma elongatum, Agardh. ...		+					+							+													
Fragilaria crotonensis, Kitton ...		O		F	C	+	O		F		+		O	+		+				O							
F. capucina, Desm. ...		+	+		+	+	+	+		+		+		+		+											
Asterionella formosa, Hass. ...		+		C	O	+	+	+	F	C	O	O	O	+		+	F			+		F	C	O	C	O	
A. formosa var. *acaroides*, Lemm. ...													+		+												
Synedra acus var. *angustissima*, Grun.												A						C	C								
S. acus. var. *radians* (Kütz.), Hust.		+	+			+			+	+	+		+				+			+	+			+	+		
Mallomonas caudata, Iwanoff ..																							+				
Dinobryon sertularia Ehr.			+							+					+												
D. sociale **Ehr.**				+					+				+														
D. sociale var. *americanum* (Brun.) **Bachm.**					+		+						+														+

TABLE I.—*The phytoplankton exclusive of Desmids*—continued.

	Key	Gill	Bunny	Rea	Arrow	Colgagh	Erne	Carrick	Cullin	Caherglassan	Talt	Glencar	Conn	Melvin	Tirneevin	Gara	Levally	Corrib (N.)	Corrib (S.)	Beltra	Aunierin	Derryclare	Ardderry	Bofin	Oorid	Ballynahinch	Kylemore
D. sociale var. *stipitatum* (Stein.) Lemm.				+									+									+	+	+			
D. divergens, Imhof.		+	C	+	+			+	+	F			+		+	+	C	O	O	+	O	O	+	O	+	O	+
D. divergens var. *Schauinslandii* (Lemm.), Brun.															+	+	+			C			C		+	+	
D. cylindricum var. *palustre*, Lemm.																+		+							+	+	
D. bavaricum, Imhof.																		+			+		+			+	
Stichogloea Doederleinii																					+			+		+	
Peridinium volzii, Lemm.	+					C																		+			
P. willei, Huitf.-Kaas																+			+					+			
Ceratium hirundinella, *O.F.M.* ..	+	+	O	+	+	C	+	O		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Microcystis aeruginosa, Kütz. ..	+												+	C											+		
M. flos aquae (Wittr.), Kirchin. ...	+	+	+	+	+																+			+		+	
Anacystis montana (Lightf.), Dr. and Daily																									+		
Coelosphaerium Kützingianum Näg.			+		+	F							+	+				+	+					+	+		
C. naegelianum Ung.	C	+		+	+	+	O	+	+	+	O	+	O	C		+	+	+	+	+			+	+	+	+		
(with *Synechococcus endobioticus* as *epiplankter*)	+	+							+				+	+				+	+								
Gomphosphaeria lacustris Chodat ..			+	+				+						+		+		+			+						
Chroococcus limneticus, Lemm. ..	+		+	+	+	O			+					+		+					+			+			
Merismopedia tenuissima, Lemm. ..			+	+							+	+		+		+					+	+	+			+	
M. glauca (Ehr.), Näg.											+	+		+							+	+		+			
M. punctata, Meyen												+		+				+						+			
Aphanizomenon flos-aquae (L.) Ralfs.	+	+			+		+																				
Anabaena circinalis Rabenth ..	+	+		+	+				+			+	+				+			+							

TABLE I.—*The phytoplankton exclusive of Desmids.*—continued.

	Key	Gill	Bunny	Rea	Arrow	Colgagh	Erne	Carrick	Cullin	Caherglassan	Talt	Glencar	Conn	Melvin	Tirneevin	Gara	Levally	Corrib (N.)	Corrib (S.)	Beltra	Aunierin	Derryclare	Ardderry	Bofin	Oorid	Ballynahinch	Kylemore
A. flos-aquae (Lyngb.), Bréb. ...	+				+	+	+		+			+	+	+			+		+	+	+		+				
A. planctonica, Brunna.	+				+		+																				
Oscillatoria irregua, Kütz. ...					+				+				+				+		+	+							
O. aghardii, Gom.	C	+				+			+	+		O	A	+	+	+	+	O	O	+		+	+				+
O. aghardii var. *isothrix*, Skuja. ..	+								+	+		+	+				+	+									
Pandorina morum (Müll.), Bory. ...			+	+	+			+																			
Eudorina elegans, Ehr.				+				+		C			+	+	O	+	+	+							+		
Volvox aureus, Ehr.		+			C					+																	
Gemellicystis neglecta (Teiling), Skuja.				+	+				+				+	+								+					+
Pediastrum duplex, Meyen	+					+	+							+				+		+							
P. boryanum (Turp.), Menegh. ..	+		+	+		+	+			+			+					+	+					+			
P. tetras (Ehr.), Ralfs.	+			+			+																				
Scendesmus quadricauda (Turp.) Bréb.				+					+	+									+					+			
S. bijugatus (Turp.), Lagerh. ...	+			+	+																						
Crucigenia rectangularis (A. Br.), Gay.			+	+																	+						
Kirchneriella lunaris (Kirch.), Möbius.	+									+			+	+													
Dictyosphaerium pulchellum, Wood ...														+				+			+	+	+	+	+	+	+
Ankistrodesmus falcatus (Corda), Ralfs.				+	+		+	+		+		+						+			+		+	+	+		
Closteriopsis longissima, Lemm. ...					+		+					+		+													
Botryococcus braunii, Kütz. ...		+	+	+			+	+	C	+	+		+	+	+	+	+	+		+				+	+	+	+
B. protuberans, West and West ...		+											+			+											
B. sudeticus, Lemm.																								+			+

TABLE II.—*The Desmid Plankton.*

Key	Bunney	Roa	Arrow	Gill	Erne	Colgagh	Garrick	Cullin	Caherglassan	Glencar	Conn	Melvin	Talt	Tirneevin	Gara	Levally	Corrib (N.)	Corrib (S.)	Aunierin	Belfra	Ardderry	Bofin	Oorid	Ballynahinch	Derryclare	Kylemore
Closterium aciculare var. *subpronum* ...					+			+		+		+				+			+	+						+
C. setaceum ...		+																	+							
Cosmarium granatum ...			+	+							+															
C. depressum ...													+		+		+	+								
C. humile ...			+	+			+																			
C. contractum ...																										
C. contractum var. *ellipsoideum* ...																										
C. alpestre ...																										
C. pseudoprotuberans ...																										
Cosmocladium saxonicum ...															+											
Spondylosum planum ...																										
Hyalotheca mucosa ...							+																			
Euastrum denticulatum ...																										
E. elegans ...																										
Xanthidium antilopeum var. *depauperatum* ...																										
Staurodesmus joshuae ...																+			+	+	+	+	+	+	+	+
S. subtriangularis ...																+			+	+	+	+	+	+	+	+
S. triangularis ...																+			+		+	+	+			
S. triangularis var. *inflatus* ...																					+	+	+			
S. curvatus ...																			+		+	+	+	+	+	+
S. curvatus var. *elongatus* ...																			+		+	+	+			
S. cuspidatus var. *candadense* ...																					+	+	+	+		
S. dejectus ...																						+	+			

TABLE II.—*The Desmid Plankton*—continued.

	Key	Bunney	Rea	Arrow	Gill	Erne	Colgagh	Carrick	Cullin	Caherglassau	Glencar	Conn	Melvin	Talt	Tirneevin	Gara	Levally	Corrib (N.)	Corrib (S.)	Aunierin	Beltra	Ardderry	Bofin	Oorid	Ballynahinch	Derryclare	Kylemore
S. dejectus var. *inflatus* ...											+		+														
S. megacanthus ...																				+		+	+	+			
Staurastrum chaetoceras ...						+		+																			
S. cingulum ...																			+	+		+	+	+	+		+
S. cingulum var. *obesum*[2] ...				+						+						+	+	+	+		+					+	
S. sebaldi var. *ornatum* ...																+		+	+								
S. sebaldi var. *ornatum f. planctonicum*				+		+						+			+					+							
S. planctonicum var. *bulbosum*																											
S. dorsidentiferum ...																		+	+								
S. longipes ...																									+	+	+
S. longipes var. *contractum*																											
S. longipes fac. *quadrata*[2]									+			+	+			+		+	+	+							
S. lunatum var. *planctonicum*											+		+														
S. furcigerum[2] ...											+	+							+	+							
S. brevispinum ...												+					+	+	+								
S. anatinum (several forms)[2]																+	+	+	+	+	+	+	+				
S. anatinum var. *grande* ...																						+					
S. anatinum var. *truncatum*																											
S. pinque ...																+	+				+				+	+	+
S. avicula ...																				+				+			
S. aversum ...																				+		+		+			
S. longispinum ...																							+	+	+		
S. denticulatum ...																					+		+	+		+	+

[2] See Brook (1958).

areas and resemble in many features the purely limestone loughs. Loughs Levally and Beltra also lie in basins which are partly limestone, but the proportion of their inflow derived from acid, mainly peat-covered rock, is higher, especially L. Beltra. Lough Talt lies in a basin and catchment area composed almost entirely of micaschist, but several features indicate that bands of metamorphic limestone, and areas of calcareous drift, have a considerable effect on the composition of the water. The Connemara loughs (Kylemore, Ballynahinch, Derryclare, Bofin, Ardderry, Aunierin and Oorid) lie on schist or gneiss, with substantial areas of blanket-bog in their catchment areas, and are therefore largely dependent on rain and blown dust for their low ionic content.

THE PHYTOPLANKTON—GENERAL DISTRIBUTION.

The distribution of the non-desmid euplanktonic species is shown in Table I, and that of the desmids in Table II. Tables VI and VII list the less widely distributed euplanktonic taxa and also the tychoplanktonic species.

Only the diatom *Asterionella formosa* and the peridinian *Ceratium hirundinella* are present in all the loughs, though there are also one or more representatives of all the other main algal groups distributed throughout a wide range of lough types, which suggests that they too are tolerant of a wide range of nutritional conditions (e.g., the isokont *Eudorina elegans*, the Chlorophycean *Botryococcus braunii*, the blue greens *Anabaena flos aquae* and *Merismopedia tenuissima*, the chrysophycean *Dinobryon divergens*, the diatoms *Cyclotella comta* and *Synedra acus* var. *radians* and the desmids *Staurastrum cingulum* var. *obesum* and *Cosmarium humile*). A considerable number of taxa are, however, limited in their distribution to loughs of a definite trophic type while the remainder show no clear affinities.

DISTRIBUTION OF BACILLARIOPHYCEAE.

Twenty-five diatom taxa were found, belonging, with the exception of *Campylodiscus*, to the Centricae or Pennatae-Araphidiales. Although taxa of the Pennatae-Biraphidiales are often considered to be components of the euplankton, they were so sporadic in occurrence that they must be regarded as tychoplanktonic.

The division of the lakes into eutrophic, mesotrophic and oligotrophic types is based on an assessment of Nygaard's Compound Index (Nygaard, 1949) (see Table III and p. 177). *Asterionella formosa*, *Cyclotella comta* and *Synedra acus* var. *radians* extend throughout the three trophic groups, which range from the highly eutrophic Lough Key (compound index 21) to the probably dystrophic Lough Ballynahinch (compound index less than 0·2). A few species are frequent in the nutrient-rich loughs but also occur in some of the waters of oligotrophic character. *Fragilaria crotonensis* is the most striking example of this, though the various taxa of the genus

Tabellaria and in particular *T. flocculosa* var. *flocculosa*, also extend from the eutrophic into the oligotrophic loughs. The latter is the only diatom which is noticeably abundant in the nutrient-poor waters, though it must be emphasised that no diatom species is restricted to the oligotrophic waters.

Of the eight oligotrophic loughs one, L. Beltra, has two eutraphentous [3]

TABLE III.—*Nature of the main drainage influence and the trophic status of the loughs in terms of the compound phytoplankton quotient.*

Lough	Drainage Influence	Phytoplankton Quotient	Trophic Status
Ballynahinch ...	Peat	4/21 = 0·19	Oligotrophic
Oorid	,, ...	6/19 = 0·3	,,
Ardderry	,, ...	7/17 = 0·4	,,
Bofin	,, ...	10/20 = 0·5	,,
Kylemore	,, ...	5/9 = 0·55	,,
Derryclare ...	,, ...	5/9 = 0·55	,,
Aunierin ...	,, ...	10/16 = 0·6	,,
Beltra	Partly limestone ...	9/13 = 0·7	Mesotrophic
Tirneevin	Limestone	1/1 = 1·0	Mesotrophic
Corrib (south) ...	Partly limestone ...	13/12 = 1·1	,,
Corrib (north) ...	,, ,, ...	16/15 = 1·0	,,
Gara	,, ,, ...	8/8 = 1·0	,,
Levally	,, ,, ...	8/7 = 1·1	,,
Talt	Limestone ...	6/2 = 3·0	Eutrophic
Melvin	,, ...	18/6 = 3·0	,,
Conn	Partly limestone ...	14/4 = 3·5	,,
Glencar	Limestone ...	16/4 = 4·0	,,
Caherglassan ...	,, ...	9/2 = 4·5	,,
Cullin	,, ...	10/2 = 5·0	,,
Carrick	,, ...	10/2 = 5·0	,,
Bunny	,, ...	13/2 = 6·5	,,
Rea	,, ...	20/3 = 6·7	,,
Erne	,, ...	15/2 = 7·5	,,
Colgagh	,, ...	8/1 = 8·0	,,
Gill	Partly limestone ...	9/0 = 9·0	,,
Arrow	Limestone ...	19/2 = 9·5	,,
Key	Shale and sandstone	21/1 = 21·0	,, (scme pollution?)

[3] i.e., species found most frequently in eutrophic waters.

species, *Tabellaria flocculosa* var. *asterionelloides* and *Fragilaria crotonensis*, common in its plankton. This is an aberrant lough in other respects (see later). Of the species restricted to the waters of high compound quotient, *Melosira varians*, *M. granulata*, *Stephanodiscus astrea* and *Asterionella formosa* var. *acaroides* do not even extend into the mesotrophic loughs (compound quotients of about 1·0) and appear to be reliable indicators of eutrophy.

Melosira italica subsp. *subarctica*, *Tabellaria flocculosa* var. *asterionelloides* and *Fragilaria crotonensis* are all fairly abundant in the eutrophic and mesotrophic loughs, whilst *Fragilaria capucina*, *Diatoma elongatum* and *Synedra acus* var. *angustissima* also occur.

DISTRIBUTION OF CHRYSOPHYCAE.

Only *Dinobryon divergens* is present in all the oligotrophic, mesotrophic and the majority of the eutrophic loughs. The variety *schauinslandii*, *Dinobryon cylindricum* var. *palustre* and *D. bavaricum* are, however, confined to the meso- and oligotrophic waters. *D. sociale* and its var. *americanum* and *D. sertularia* occur in loughs of higher nutrient status, whilst the var. *stipitatum* is found in both eutrophic and oligotrophic waters. The genus *Mallomonas* is uncommon with *M. caudata* confined to the oligotrophic waters. *Stichogloea doederleinni*, now classed amongst the Chrysosphaerinae (Huber-Pestalozzi, 1941), also occurs in three of the oligotrophic loughs.

DISTRIBUTION OF DINOPHYCEAE.

The only conspicuous species in this group is *Ceratium hirundinella*, present in all but one lough. Apart from the rare occurrence of the type *scotticum* in two of the loughs, the species exhibits little of its usual variation. *Peridinium willei* occurs in two mesotrophic and one oligotrophic lough, *P. volzii* in the eutrophic L. Colgagh and also in the markedly eutrophic L. Key and the oligotrophic L. Bofin.

DISTRIBUTION OF CYANOPHYCEAE.

This group is more common in the eutrophic loughs. Only one species, *Anacystis montana*, is restricted to the oligotrophic series, whilst the following are almost completely confined to the eutrophic loughs : *Microcystis* spp., *Aphanothece stagnina*, *Oscillatoria lacustris*, *Lyngbya limnetica*, and *Anabaena planctonica*. The species *Gomphosphaeria aponina*, *G. lacustris*, *Oscillatoria bornetii* and *O. irrigua*, are all of limited occurrence, extending into the mesotrophic loughs, whilst the remaining taxa and especially the *Merismopedia* spp. extend their range even further into the oligotrophic waters. The most common species of Cyanophyceae are *Coelosphaerium naegelianum* and *Oscillatoria agardhii*.

Distribution of Chlorophyceae (exclusive of Desmidiae).

The majority of these have a wide distribution in the eutrophic loughs. Of the motile Volvocales, only *Eudorina elegans* extends into the oligotrophic waters whilst *Volvox aureus* and *Pandorina morum* are confined to the eutrophic. *Volvox* is an important component of the plankton in Lough Arrow. The Isokont *Gemellicystis neglecta* which Lund (1956) states is common in many " neither very strongly eu- nor oligotrophic lakes " has been found in the present collections in five of the loughs with quotients indicative of eutrophy and also in the moderately oligotrophic Kylemore Lough.

The remaining species of Chlorophyceae are the characteristically eutrophic Chlorococcales of which *Closteriopsis longissima*, *Oocystis lacustris*, *Scenedesmus tetras*, *S. bijugatus*, *S. arcuatus*, *Kirchneriella lunaris* and *Elakatothrix gelatinosa* are confined to the eutrophic series. The colonial species *Dictyosphaerium pulchellum* is present in all the oligotrophic loughs (except L. Beltra) and extends only into the mesotrophic L. Corrib and the slightly eutrophic L. Melvin, whilst *Coelastrum microporum*, *Troschisca planktonica* and the dubious species, *Elakotothrix linearis* also occur in this series.

Three species of the genus *Botryococcus* have been recorded. This was classified by Pascher (1925) as a heterokont but is now included in the Chlorophyceae (Blackburn and Temperley, 1932 ; Belcher and Fogg, 1955). *B. braunii* is the most common and widely distributed, occurring in more than half of the oligotrophic loughs, in all but one of the mesotrophic, and in about three-quarters of the eutrophic. It appears to be commoner in the more eutrophic waters. In three loughs of this latter type, forms of *Botryococcus*, which may be referred to the doubtful species, *B. protuberans*, have been found, whilst the rare *B. sudeticus* occurs in two of the oligotrophic series.

Distribution of Desmideae.

It can be seen from Table II, in which the distribution of the more widely occurring desmids is given, that many of the loughs support a considerable number of species and varieties of this group. In all, more than 110 taxa have been recorded from the 26 loughs sampled and only in one (L. Gill) have no desmids been found, though many of the eutrophic waters contain only one or two species. Of the taxa identified about 50 are rare and may be regarded as tychoplanktonic.[4] These, with the more uncommon plankton desmids, have been listed in Tables VI and VII. By far the richest desmid flora was found in Lough Bofin, from which about 80 distinct taxa have been listed, though of this number, 50 are tychoplanktonic.

Of the true plankton desmids, 5 forms show clear eutrophic affinities. These are *Closterium aciculare* var. *subpronum*, *Cosmarium granatum*, *Staurodesmus dejectum* var. *inflatum*, *Staurastrum chaetoceras* and *S. sebaldi* var. *ornatum* f. *planctonicum*.

[4] Derived from other communities and present in the plankton for short periods.

Two taxa appear to tolerate an especially wide range of trophic conditions, both *Cosmarium humile* and *Staurastrum cingulum* var. *obesum* being scattered throughout the whole range of water types. With reference to the latter variety, it is interesting to note that the type species, *S. cingulum*, has been found only in the samples from loughs which appear to be distinctly oligotrophic.

As is general with Desmids, most of the species are restricted to oligotrophic waters, though there are exceptions. Of special interest in this respect is *Staurastrum longipes*. The type species and the var. *contractum* seem to occur only in oligotrophic waters, whilst a somewhat robust and quite distinctive quadriradiate form, recorded in Table II as *S. longipes* fac. *quadrata* (see Brook, 1958, Figs. 48 and 49), was frequent in the samples from six loughs in the middle of the trophic range, and rare in the oligotrophic Ballynahinch.

Other taxa which are abundant in the oligotrophic loughs, but which also occur in some of the waters of apparently richer status, are *Cosmarium depressum*, *Staurodesmus dejectum*, *Staurastrum lunatum* var. *planctonicum*, *S. brevispinum* and *S. furcigerum*.

A CLASSIFICATION OF THE LOUGHS.

The loughs have been classified in Table III in terms of Nygaard's Compound Phytoplankton Quotient (Nygaard, 1949), which is the sum of the number of species of Chlorococcales, Myxophyceae, Centric diatoms and Eugleninae, divided by the number of Desmid species in each sample. In using this quotient, which has been found to give a fairly reliable index of the trophic status of a body of water, only true plankton species must be considered. In general terms, waters with quotients of less than one may be regarded as oligotrophic while those greater than one are considered to be eutrophic ; the higher the quotient, the richer the water. Between the categories oligo- and eutrophic, Nygaard states that waters with quotients of between 1 and 2·5 should be termed mesotrophic. Lakes with very low quotients (less than 0·2) may be regarded as dystrophic. Thus Table III shows that the loughs sampled during the present investigation exhibit a wide range of trophic status as indicated by these quotients, ranging from the apparently dystrophic Ballynahinch (0·19) to the highly eutrophic Key and with Tirneevin, Gara, Corrib and Levally, all of mesotrophic status. The loughs with mainly peaty drainage are clearly oligotrophic, while Lough Beltra, although it has some limestone influence in its drainage, must also be placed in this category with a quotient of 0·7.

In addition to the characterisation of lake plankton by an index such as that provided by Nygaard's Compound Phytoplankton Quotient, it has been found (Thunmark, 1945) that a comparison of lakes in terms of their dominant plankton taxa can be of considerable value. This is especially applicable when, as in the present investigation, all the waters being investigated have been sampled within a few days of one another and collections are therefore representative of this community at a particular

season, in the present case, late summer. At this time the following were dominant constituents of the plankton in the 26 loughs under investigation:—

EUTROPHIC.

Key : *Oscillatoria agardhii, Coelosphaerium naegelianum.*
Arrow : *Melosira granulata, Volvox aureus.*
Gill : *Fragilaria crotonensis.*
Colgagh : *Peridinium voltzii, Ceratium hirundinella.*
Erne : *Melosira granulata, Fragilaria crotonensis, Coelosphaerium naegelianum.*
Rea : *Asterionella formosa.*
Bunny : *Asterionella formosa, Dinobryon divergens.*
Carrick : *Melosira italica* subsp. *subarctica, Tabellaria flocculosa* var. *asterionelloides, Hyalotheca mucosa.*
Cullin : *Botryococcus braunii, Fragilaria crotonensis, Asterionella formosa.*
Caherglassan : *Eudorina elegans, Asterionella formosa.*
Glencar : *Synedra acus* var. *angustissima, Melosira italica* subsp. *subarctica.*
Conn : *Oscillatoria agardhii.*
Melvin : *Coelosphaerium naegelianum, Microcystis aeruginosa.*
Talt : *Asterionella formosa.*

MESOTROPHIC.

Tirneevin : Plankton too sparse to describe accurately.
Levally : *Asterionella formosa, Dinobryon divergens.*
Gara : *Tabellaria flocculosa* var. *asterionelloides.*
Corrib (North and South) : *Synedra acus* var. *angustissima.*

OLIGOTROPHIC AND DYSTROPHIC.

Beltra : *Tabellaria flocculosa* var. *asterionelloides, Dinobryon divergens* var. *schauinslandii.*
Aunierin : *Spondylosum planum, Staurodesmus triangularis var. inflatus, Staurastrum longipes.*
Derryclare : *Staurastrum anatinum.*
Kylemore : *Staurastrum anatinum, Staurodesmus cuspidatus* var. *canadense.*
Bofin : *Staurastrum longipes, Cosmarium contractum.*
Ardderry : *Asterionella formosa, Dinobryon divergens* var. *schauinslandii.*
Oorid : *Staurastrum longipes, Staurodesmus triangularis* var. *inflatus.*
Ballynahinch : *Staurastrum anatinum, Asterionella formosa.*

Of the eutrophic loughs, the two extremely calcareous waters, L. Bunny and L. Rea, all have *Asterionella formosa* as their absolute dominant. L. Talt, also with *Asterionella formosa* dominant, is grouped with these two, for although lying in a basin of mica schist it is obviously greatly affected by surrounding calcareous strata and deposits. Key with the highest trophic index, and Conn and Melvin, whose quotients are amongst the lowest of the

eutrophic loughs, are all dominated by Cyanophyceae. Glencar (eutrophic index) is dominated by the diatom *Synedra acus* var. *angustissima*, as is the apparently mesotrophic Corrib. Both of these loughs are on similar rock formations, though Corrib has, in addition to limestone, some metamorphic rocks bordering parts of its shoreline; Arrow, Erne and Gill are dominated by the eutraphentous *Melosira granulata* and *Fragilaria crotonensis*. These three and the previously mentioned Glencar and Corrib form a subgroup characterised by the dominance of eutraphentous diatoms. Colgagh is the only lough in which a Dinoflagellate, *Ceratium hirundinella*, is dominant, although this is one of the most widespread species throughout the loughs. Carrick is also unusual amongst the eutrophic series in that the filamentous desmid, *Hyalotheca mucosa*, is dominant. It should be noted, however, that its subdominants, *Melosira italica* subsp. *subarctica* and particularly *Tabellaria flocculosa* var. *asterionelloides*, are mesotraphentous rather than eutraphentous. The two remaining eutrophic loughs, Cullin and Caherglassan, have *Botryococcus braunii* and *Eudorina elegans*, respectively, as dominants, whilst *Asterionella formosa* is sub-dominant in both and *Fragilaria crotonensis* an additional sub-dominant in Cullin.

In the mesotrophic group, Gara and Levally have oligotraphentous, and Corrib eutraphentous dominants.

The late summer plankton of most of the oligotrophic loughs is dominated by desmids, exceptions being Beltra and Ardderry.

Resulting from the above analysis of dominance the loughs have been regrouped in Table IV according to their dominant taxa. This re-grouping seems to confirm the broad classification of the loughs as derived from the determinations of the Compound Phytoplankton Quotients, and, in addition, fits fairly closely a classification based on information available concerning the geological strata and soil conditions in the drainage area of the loughs.

TABLE IV.

Oligotrophic.

Desmids dominant: Ballynahinch, 0·2; Oorid, 0·3; Bofin, 0·5; Aunierin, 0·6.

Desmids dominant, with some eutraphentous spp.: Derryclare, 0·55; Kylemore, 0·55.

Tabellaria-Dinobryon-Asterionella-Desmids frequent: Ardderry, 0·4; Beltra, 0·7.

Mesotrophic.

Tabellaria-Dinobryon-Asterionella dominant: Gara, 1·0; Levally, 1·1.

Synedra acus var. *angustissima* dominant: Corrib (North), 1·0; (South) 1·1.

Eutrophic.

Synedra acus var. *angustissima* dominant: Glencar, 4·0.

Eudorina elegans-Asterionella dominant: Caherglassan, 4·5.

Melosira italica subsp. *subarctica*, *T. flocculosa* var. *asterionelloides* dominant : Carrick, 5·0.
Botryococcus-Asterionella dominant : Cullin, 5·0.
Asterionella formosa dominant : Talt, 3·0 ; Bunny, 6·5 ; Rea, 6·7.
Dinoflagellates dominant : Colgagh, 8·0.
Fragilaria crotonensis dominant : Gill, 9·0.
Oscillatoria-Coelosphaerium dominant : Conn, 3·5 ; Melvin, 3·0 ; Key, 21·0.
Melosira granulata dominant : Erne, 7·5 ; Arrow, 9·5.

The loughs where the Compound Quotient is 1·0 (the border between oligotrophy and eutrophy), appear, on the basis of dominant species, to be divided into the waters which have Desmids or *Tabellaria*, *Dinobryon* and *Asterionella*, and those with *Synedra*, *Asterionella*, *Fragilaria*, *Melosira* or blue-green species abundant. Thus it seems that the category mesotrophic is not a useful grouping, at least for the loughs considered here. The loughs in this category should therefore be classed either as oligotrophic or eutrophic depending on the dominants in their plankton ; thus on this basis Gara and Levally are oligotrophic and Corrib eutrophic. The oligotrophic series is divided into two groups, one dominated by desmids and one probably of higher trophic status dominted by *Tabellaria*, *Dinobryon* and *Asterionella*. Five sub-groups may be recognised in the eutrophic series, dominated respectively by *Synedra*, *Asterionella* (*Botryococcus* and *Eudorina* in Caherglassan and Cullin respectively are thought to be temporary local outbursts), *Fragilaria*, *Oscillatoria-Coelosphaerium* and *Melosira*. These latter sub-groups, see Table IV, do not fit closely with the grouping of the loughs as indicated by their Phytoplankton Quotients. Similar discrepancies were found by Nygaard (1949) in investigations of Danish lakes. Since species dominance is a much less constant factor than the specific composition of a plankton, the former often altering completely within a short time, it is believed that any classification of lakes on the basis of their dominant taxa must be treated with reserve. However, as Nygaard suggests, considered in conjunction with the corresponding phytoplankton quotient it may be of some value.

TABLE V.

Taxonomic Group	Average number of species per lough		
	Eutrophic loughs	Mesotrophic loughs	Oligotrophic loughs
Chlorococcales ...	3·5	1·8	2·5
Myxophyceae ...	7·2	5·2	3·1
Centric diatoms ...	2·7	1·8	0·9
Desmideae	2·4	8·6	15·5
Pennate diatoms ...	5·6	5·4	3·7
Chrysophyceae ...	1·2	2·8	3·3
Dinophyceae	1·3	1·4	1·4

Table V shows the average number of species per lough in each of the three trophic categories for each of the principal taxonomic divisions considered. Since the separation of the loughs into these categories is based on the proportions of Chlorococcales, Myxophyceae and Centric Diatoms to Desmids, it is to be expected that species in the former groups predominate in the eutrophic waters and desmids in those of oligotrophic status. Myxophyceae and Centric Diatoms exhibit a much greater difference between the three trophic categories than Chlorococcales, and thus would seem to be more valuable as indicators of trophic status. The analysis of the distribution of Pennate diatoms and Chrysophyceae which are not included in Nygaard's Compound Quotient, clearly indicates that the former group is another indicator of eutrophy whilst Chrysophyceae, as a whole, are most numerous in poorer waters. The number of taxa of Dinophyceae in all the loughs is so small that it is not possible to make any deductions about their trophic affinities.

Thunmark (1945a) suggested that the ratio between Chlorococcales and Desmids, which is termed the chlorophycean quotient by Nygaard (1949), is an important characteristic of plankton communities. Comparison of the average number of species of Chlorococcales and Desmideae in the Irish Loughs (Table V) with the diagram Abb. 6 (Thunmark, 1945 (b), p. 57) showing the relationship between these two groups and the trophic status of some Swedish lakes, illustrates the quantitative difference between the phytoplankton of these two regions. The Swedish eutrophic lakes have between 20–50 Chloroccalean species, compared with an average of 3·5 in the Irish loughs (see Table V) and the oligotrophic lakes of Fiolen type have 20–35 Desmid species compared with an average of 15·5 in the Irish oligotrophic loughs. Thus the Chlorococcales : Desmids quotient is approximately 4·5 and 0·14 for the eutrophic Swedish and Irish loughs respectively and 0·3 and 0·016 for the oligotrophic loughs. Although the number of species are very different in the waters of the two regions, the ratios are comparable. Definite numerical values for various trophic states cannot be devised so easily for this quotient as for the compound quotient. Nygaard (1949) gives the chlorophycean quotient of some oligotrophic Danish lakes as 0–0·7, of mesotrophic 0·2–0·6 and eutrophic 0·7–3·5 (p. 14) ; on this basis all the Irish loughs would be oligotrophic. Although in general it is true that there are a high number of Chlorococcalean species in eutrophic lakes and a high number of Desmids in oligotrophic lakes, some species within these groups are indicative of quite contrary conditions, e.g., *Closterium aciculare* var. *subpronum* is more common in eutrophic habitats and *Dictyosphaerium pulchellum* in oligotrophic.

In late August and early September, 1904, West and West collected plankton from some small loughs between Clifden and Roundstone, which are in the region from which the present samples, dominated by desmids were obtained. They also collected from loughs Corrib, Cullin and Conn. Comparison of the 1904 lists with the present data shows little change in dominance and no change in trophic status for these loughs. In 1904 the small oligotrophic

loughs were dominated, as in this recent investigation, by desmid species and *Ceratium hirundinella* was common ; L. Corrib supported *Synedra acus* var. *angustissima* (*S. lemmermanni* of West and West), *Asterionella formosa*, *Gomphosphaeria lacustris*, and *Cyclotella schroeteri* in 1904, whilst in 1953 *Oscillatoria agardhii* and *Tabellaria* spp. replace the two latter species ; in L. Cullin *Asterionella formosa* is still abundant whilst the *Anabaena* spp. and *Ceratium hirundinella* are less conspicuous. L. Conn still has some *Asterionella formosa* but neither *Melosira varians* nor Cyanophyceae were common in the 1953 samples.

The distribution of species in the different trophic groups is similar to that recorded by Pearsall and Lind (1942–3), except that *Tabellaria flocculosa* v. *asterionelloides* is not so widely dispersed in loughs with both calcareous and acidic drainage, and the above authors did not record any *Melosira* spp. from their loughs. This latter feature may be related to the size of the loughs, since on the whole they sampled in smaller bodies of water, whereas most of the 1953 samples were obtained from loughs of considerable size.

TABLE VI.—*Plankton species of Limited Distribution, not recorded in Table I.*

BACILLARIOPHYCEAE:

Melosira ambigua (Grun.), O. Mull.	L.
M. italica var. *valida*, Grun.	Gl.
Cyclotella comensis, Grun.	C (s).
C. glomerata, Bachm.	C (n).
Stephanodiscus hantzschii, Grun.	E.
Coscinodiscus lacustris, Grun....	Ar.
Synedra ulna var. *danica* (Kutz.), Grun.	Ar., M.
Nitzschia acicularis, W. Sm.	Conn, E., Tv.
Campylodiscus noricus var. *hibernica* (Ehr.), Grun. ...	Gl.

CHRYSOPHYCEAE:

Mallomonas longiseta, Lemm.	Au.
M. producta, Iwanoff	Au.
D. divergens var. *angulatum* (Sel.), Brunn.	Bu.
D. cylindricum var. *alpinum* (Imhof), Bachm. ...	Ga.
D. bavaricum var. *vanhoffenii* (Bachm.), Krieger ...	C (n).

DINOPHYCEAE :

Peridinium tab. contactum var. *excavatum* (Play.), Lef.	R.
C. hirundinella typus scotticum, Bachm.	Bu., Ca.
C. cornutum (Ehr.), Clap. et Lachm.	Ta, Bo.
C. carolinianum (Bailey), Jorgensen	Bo.

TABLE VI.—(*continued*).

CYANOPHYCEAE :

Aphanothece stagnina (Spreng.), A. Br.	E.
A. clathrata, West and West...	R., Ar., Be.
Rhabdoderma lineare, Schmidle et Lauterb.	Ar.
Gomphosphaeria aponina, Kutz.	Ca.
Eucapsis alpina, Clem. and Shantz	Ta.
Holopedia geminata, Lagh.	R.
Chroococcus dispersus var. ***minor*** G. M. Sm.	Gl., Col., Bu
Anabaena aequalis, Borge	E.
Oscillatoria lacustris (Kleb.), Geitler	K.
O. limnetica, Lemm.	C (s), R.
O. bornetii, Zukal	R., Ga.
Lyngnya limnetica, Lemm.	Gl.

CHLOROPHYCEAE :

Pediastrum araneosum (Racib.), G. M. Sm.	C (n).
P. duplex var. *rugulosum*, Racib.	C (s).
Oocystis lacustris, Chod.	Ar.
O. solitaria, Wittr.	R., Bu.
Scenedesmus arcuatus, Lemm.	R.
S. denticulatus, Lagerh.	Ad., Bu.
S. obliquus (Turp.), Kutz.	Bu.
S. opoliensis, P. Richter	K.
Tetraedron gracile (Reinsch), Hansg.	Car.
Crucigenia quadrata, Morren	C (n)., Av.
Kirchneriella obesa (West), Schmidle	M., K.
Coelastrum microporum, Naeg.	Bo.
Troschiscia planctonica, Lind and Pearsall	D.
Elakatothrix gelatinosa, Wille	R.
E. linearis, Pascher ?	Ar.
Stylosphaeridium stipitatum	M.

TYCHOPLANKTONIC SPECIES :

Synedra ulna (Nitzsch.), Ehr.	K.
Ceratoneis arcus, Kutz.	C (s).
Mastogloia spp.	Ta.
Denticula tenuis, Kutz.	K., Ta., C (s).
Cymatopleura solea (Breb), W. Sm.	K.
C. elliptica (Breb.), W. Sm.	M., B.
C. elliptica var. *hibernica* (W. Sm.), Hust.	K.
Surirella biseriata, Breb.	Con., M., B.
S. biseriata var. *bifrons* (Ehr.), Hust.	Ta.
Gloeotrichia echinulata (J. E. Sm.), P. Richter ...	Gi.
Cylindrospermum stagnale (Kg.), Born. et Flah. ...	Gl.
Tribonema viride, Pascher	Ca.
Ulothrix spp.	O.
Spirogyra spp.	E., Ga.
Mougeotia spp.	Ga., E., Cu., Co., Tu.
Zygnema spp.	Ga., B.

TABLE VII.—*Additional Desmid species, mostly tychoplanktonic, not recorded in Table II.*

Closterium gracile, Breb.	B.
——————— var. *elongatum*, West and West	B.
C. lanceolatum, Kutz.	L.
C. venus, Kutz.	K., B.
Netrium digitum (Ehr.), Itzigh. and Rothe.	O.
N. oblongum	B.
Tetmemorus brebissonii (Menegh.), Ralfs	B.
Euastrum denticulatum (Kirch.), Gay	B., O.
E. elegans (Breb.), Kutz.	B., Au.
E. insulare (Wittr.), Roy forma	Rea.
E. obesum, Josh.	B.
E. verrucosum, Ehr.	Ar.
E. pectinatum var. *inevolutum*, West and West	Au.
Micrasterias conferta, Lund.	B.
M. denticulata, Breb.	B.
M. pinnatifida (Kutz.), Ralfs	B.
M. radiata, Hass.	O.
M. sol (Ehr.), Kutz.	Ard., B.
M. truncata (Corda), Breb.	Bally, B.
Cosmarium alpestre, Roy and Biss.	Aun., B.
C. entochondrum, West and West	B.
C. formulosum, Hoff.	Rea
C. globosum, Bulnh.	Gara
C. margharitiferum, Menegh.	B.
C. moniliforme (Turp.), Ralfs	Bun.
C. punctulatum, Breb.	Cah.
C. quinarium, Lund.	B.
C. rectangulare, Grun.	B.
C. reniforme (Ralfs), Arch.	B.
C. tetraopthalmum, Breb.	Bun.
C. subtumidum var. *klebsii* (Gutw.), W. and W.	Colg.
Xanthidium antilopeum (Breb.), Kutz.	B.
——————— var. *hebridarum*, West and West	B.
——————— var. *polymazum*, Nordst	B.
X. cristatum var. *uncinatum*, Breb.	B.
Staurodesmus bulnheimii (Racib.) nov. comb.	B.
S. convergens (Ehr.), Lillieroth	B.
S. crassus (West), Lillieroth	B.
S. cuspidatus (Breb.), Teil.	B.
S. glabrus fac. brebissonii (Racib.), nov. comb.	B.

TABLE VII.—(*continued*).

Staurastrum alternans, Breb.	B.
S. arachne, Ralfs forma	B.
S. arctiscon (Ehr.), Lund.	B.
S. boreale, West and West	B.
S. brachiatum, Ralfs	B.
S. coniculatum var. *spinigerum*, West	B.
S. crenulatum (Nag.), Delp.	Rea, B ?
S. disputatum, West and West	B.
S. duacense, West and West	B.
S. furcigerum var. *reductum*, West and West	C (s).
———— var. *simplissisimum nov.* var.	C (s).
S. grande, Bulnh.	B.
S. inflexum, Breb.	B.
S. laeve, Ralfs	B.
S. orbiculare var. *depressum*, Roy and Biss.	B.
S. ornatum, Turn. forma ?	B.
S. pachyrhynchum, Nordst.	B.
S. pelagicum, West and West	C (s).
S. proboscidium (Breb.), Arch.	B.
S. setigerum, Cleve	B.
S. subgracillum, West and West	B.
S. tohopekaligense, Wolle	B.
Sphaerozozma aubertianum var. *archeri* (Gutw.), West and West ...	B.
S. vertebratum (Breb.), Ralfs	C (s).
Spondylosum papillosum, West and West	B.
Desmidium cylindricum, Grev.	B.
Hyalotheca dissiliens	Ball.

Abbreviations used:—

Ard. = L. Ardderry.

Au. = L. Aunierin.

B. = L. Bofin.

Ball. = L. Ballynahinch.

Bun. = L. Bunny.

Cah. = L. Caherglassan.

C (s) = L. Corrib (south).

K. = L. Key.

O. = L. Oorid.

TABLE VIII.—*The position and area of the loughs.*

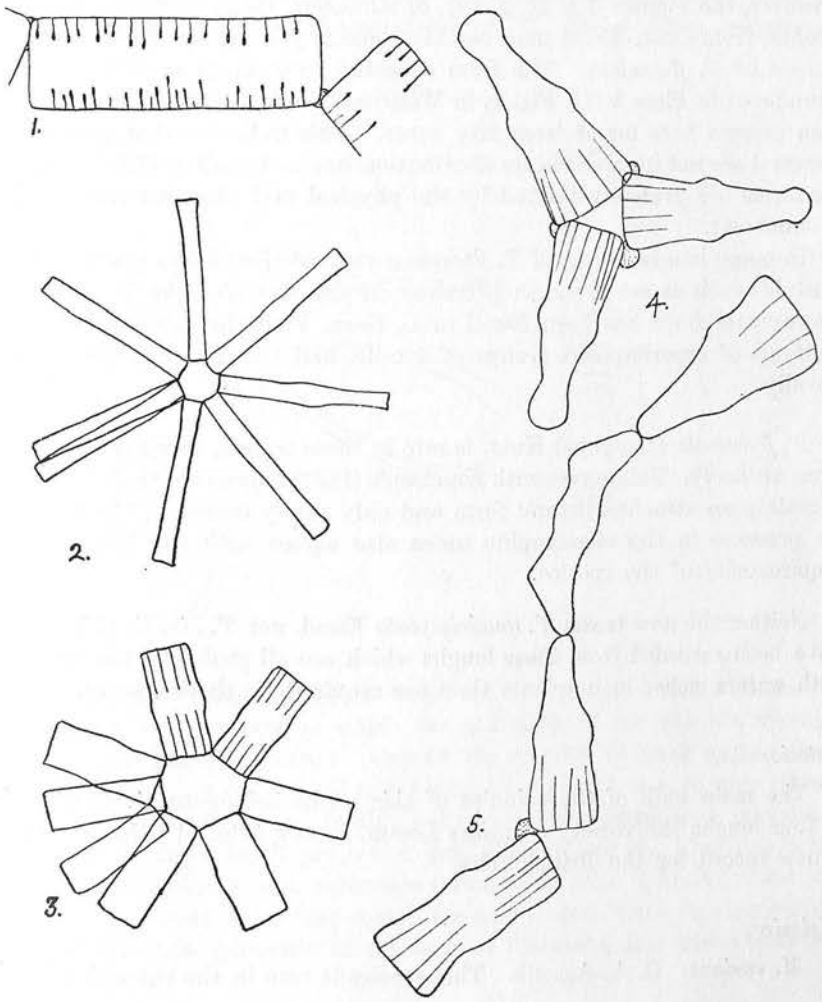
Lough	County	Irish National Grid Reference	Acres
Ardderry	Galway	L 99 46	153
Arrow	Roscommon, Sligo ...	G 7 1	3,123
Aunierin	Galway	M 01 46	53
Ballynahinch	Galway	L 78 48	410
Beltra	Mayo	M 0 9	1,074
Bofin	Galway	M 03 44	220
Bunny	Clare	R 38 97	233
Caherglassan, Turlough	Galway	M 42 06	variable
Carrick	Fermanagh	H 09 55	98
Colgagh	Sligo	G 74 36	81
Conn	Mayo	G 1 1	12,876
Corrib	Galway, Mayo ...	M 1 4	41,617
Cullin	Mayo	G 2 0	2,789
Derryclare	Galway	L 82 48	535
Erne (Lower)	Fermanagh	H 1 5	27,433
Gara	Roscommon, Sligo ...	G 7 0	4,152
Gill	Sligo, Leitrim ...	G 7 3	3,463
Glencar	Sligo, Leitrim ...	G 75 43	284
Key	Roscommon	G 8 0	2,217
Kylemore	Galway	L 77 58	346
Levally	Mayo	G 15 04	334
Melvin	Fermanagh, Leitrim ...	G 9 5	5,327
Oorid	Galway	L 94 46	146
Rea	Galway	M 61 16	755
Talt	Sligo	G 39 15	237
Tirneevin, Turlough ... (named Hawkshill Lough in O.S. 6 in. map)	Galway	M 41 02	variable

NOTES ON SOME SPECIES.

Tabellaria.

There is a wide range of forms in the Irish loughs. *T. flocculosa* var. *flocculosa* (Roth.) Knud. is found in numerous loughs but is never abundant in the plankton. The cells are usually short with a small number of septa (4–10) but in Oorid, Aunierin and Bofin, a long celled form was common and had up to 20 septa per cell (Fig. 1). The latter type of cell appears to be restricted to the more oligotrophic loughs.

There are two distinct forms of star-shaped *T. flocculosa* in Kylemore. One is a typical long celled form which may be assigned to *T. flocculosa* var. *asterionelloides* (Grun.) Knud. (Fig. 2), and is very similar in colony morphology to those forms found in Bassenthwaite and Derwentwater of



the English Lake District (Knudsen, 1955). The other is closely allied to *T. floccolosa* var. *pelagica* (Fig. 3) with which the Coniston Water forms have been associated (Knudsen, 1953 and 1955) ; this is a rather uncommon colony morphology in the Irish loughs. The presence in Ireland of these and other forms, similar to those occurring in the English Lake District, appears to contradict Knudsen's (1955) statement that: " Their small geographical ranges may be due to the fact that they are of recent origin ". Forms which are similar in colony morphology were recorded in photomicrographs of L. Neagh plankton by West and West (1906) together with a long celled form. In Conn two forms with very twisted cells are found either as star or as lax zig-zag colonies (Figs. 4 and 5). The cells have numerous septae per cell and must be assigned to varieties of *T. flocculosa*. No such colonies are figured in Knudsen's papers although it is probable that these forms are *T. flocculosa* var. *teilingii* Knud., this being based on Swedish material from Taftlången. However, the Figures 3 A–H, p. 137, of Knudsen (1953) resemble closely the colonies from Conn and it may be that there is yet another taxa within the bounds of *T. flocculosa*. The form collected from Conn in 1953 is clearly reproduced in Plate VIII, Fig. 1, in West and West (1906) and has therefore been present here for at least fifty years. This indicates that problems of dispersal are not involved in its distribution but as Knudsen (1955) suggests, the forms are probably limited by the physical and chemical nature of the environment.

In many loughs, forms of *T. flocculosa* var. *asterionelloides* possess twisted frustules such as are found in Ullswater in the English Lake District. The Haweswater form has been found in L. Gara, with the colonies sometimes built up of superimposed groups of 4 cells, and the Thirlmere form in L. Levally.

T. fenestrata (Lyngbye) Kutz, is rare in these waters, being recorded only from Ardderry. This agrees with Knudsen's (1952) comments that this species is mainly an attached littoral form and only rarely occurs in the plankton. Its presence in the oligotrophic series also agrees with the low alkalinity requirements of the species.

Neither the new taxon *T. quadriseptata* Knud. nor *T. binalis* (Ehr.) Grun. have been recorded from these loughs which are all probably too large and with waters richer in nutrients than are required by these species.

Asterionella.

The main bulk of the colonies of this genus belong to *A. formosa* but in four loughs the variety *acaroides* Lemm. occurs (Fig. 6) ; this is possibly a new record for the British Isles.

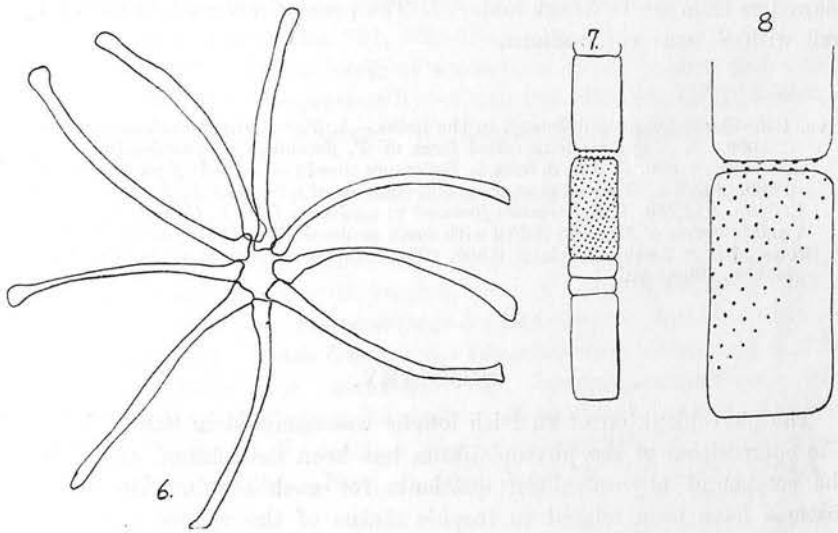
Melosira.

M. varians. C. A. Agardh. This species is rare in the eutrophic loughs.

M. granulata (E) Ralfs. is confined to the eutrophic loughs and there are forms with the end cell pores coarser than the others of the filament (Status β) and also forms with all the cells coarsely pored (Status α).

M. ambigua (Grun.) O. Mull. This species is rare in and only found in L. Levally.

M. italica (E.) Kg. Forms assignable to the subsp. *subarctica* are quite common, varying considerably in cell width and length. Most filaments have cells with 18 rows of pores in 10 μ and 18 punctae in 10μ (i.e., Status α), but there are a few filaments, each having a few cells with finer pores (Status β) and a few filaments in which all the cells are fine pored (Status γ). There are filaments in Glencar Lough which have very few rows of pores and possibly belong to the var. *valida*. Scattered in several lakes there are filaments in which the number of rows of pores is less than that given in Huber-Pestalozzi (1942) as characteristic of *M. italica* subsp. *subarctica*,



but they are not coarse enough to be placed in the var. *valida*. Forms of *M. italica* are also common in which the end teeth of the cells are missing and only small granules remain. Usually the number of teeth on the edge of the discus does not correspond to the number of pervalvar pore rows (these are generally in excess of the teeth), but in the Irish forms each pervalvar row ends in a single small projection (see Figs. 7 and 8). This has been recorded as *M. italica* subsp. *subarctica* forma until more is known about it. A. Cleve Euler (1951) states that sometimes conspicuous teeth are only found in some of the cells, generally at the ends of filaments, and that elsewhere they are absent.

Synedra.

There has been considerable confusion over the planktonic forms of this genus. West and West (1906) recorded ten different taxa from the Irish loughs, but most of them were rare except a new taxa, *S. Lemmermanni* West and West, in L. Conn. In the description of *S. Lemmermanni* the number of transverse striations is given as 10 in 10·3 μ and the length of the cell 430–440 μ. This species is given as synonymous with *S. acus* var. *angustissima* in Huber-Pestalozzi (1942), although the number of striations in this latter taxon is 13–18 in 10 μ. West and West (1906) also recorded the latter species in L. Corrib and it was still present in 1953. In 1953 the *Synedra* species in L. Conn was *S. acus* var. *radians* which is not synonymous with the Wests' *S. Lemmermanni*, but probably with *S. revaliensis* Lemm. described from L. Conn and L. Cullin by West and West as a radiating colony belonging to Lemmermann's subgenus *Belonastrum*. West and West (1906) recognised *S. radians* in L. Neagh ; this is now synonymous with *S. acus* var. *radians* and hence the radiate *Synedra* from Conn and Cullin, which they regarded as *S. revaliensis*, presumably shows slightly different characters from the L. Neagh material. The present material, however, agrees well with *S. acus* var. *radians*.

FIGS. 1–8.—Some Diatoms discussed in the notes.—1. *Tabellaria flocculosa* from L. Oorid × 2,000. 2. A typical long celled form of *T. flocculosa* v. *asterionelloides* from L. Kylemore. × 800. 3. A form from L. Kylemore closely allied to *T. flocculosa* v. *pelagica*. × 800. 4 and 5. Twisted star or zig-zag colonies of a form of *T. flocculosa* both from L. Conn. × 1,250. 6. *Asterionella formosa* v. *acaroides* from L. Caherglassan. × 1,250. 7 and 8. Forms of *Melosira italica* with small projections at the ends of the pervalvar rows. 7 is × 2,640 and 8 is × 6,600. The complete markings on the frustules have not been illustrated.

SUMMARY.

The phytoplankton of 26 Irish loughs was sampled in September, 1953. The composition of the phytoplankton has been determined and from this the compound phytoplankton quotients for each lough. Both of these features have been related to trophic status of the waters and as far as possible to the surrounding vegetation and geology. Notes on some species (other than desmids which have been dealt with elsewhere, Brook, 1958) have been given.

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NOTES ON DESMIDS OF THE GENUS *STAURASTRUM* III

BY
A. J. BROOK

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NOTES ON DESMIDS OF THE GENUS *STAURASTRUM*

III. *STAURASTRUM PARADOXUM* MEYEN IN THE JENNER HERBARIUM OF THE BRITISH MUSEUM

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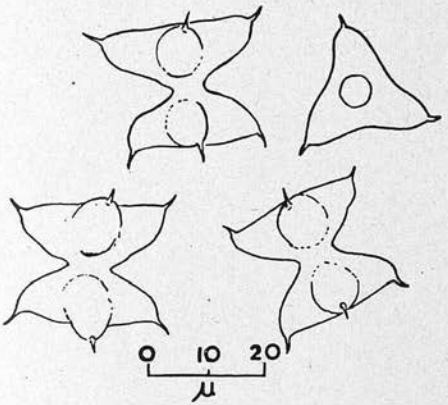
In an attempt to determine the identity of the desmid referred to as *S. paradoxum* Meyen by Ralfs in his monograph, *British Desmidieae* (1848), the mica from a packet in the Jenner Herbarium of the British Museum has been examined. It is labelled in the following way:

Staurastrum paradoxum
Staurastrum mucronatum
Penzance.

Mr. R. Ross, Keeper of the Cryptogamic Herbarium of the Museum, has commented that this is almost certainly part of the material examined by Ralfs when preparing his monograph.

The material on the mica would seem to be a squeezing or scraping from plants collected from a ditch or the margin of a pond and contains a considerable amount



Staurodesmus dejectus (Ralfs) Teiling

of silt and detritus. Attached diatoms are fairly common (e.g. *Eunotia* spp., *Epithemia* spp., *Tabellaria* spp., etc.) and three desmids are very frequent. These are *Euastrum binale*, a very small *Staurastrum* and *Staurodesmus dejectus* (Breb.) Teiling (=*Staurastrum dejectum* Breb.). No monospinous desmid with 'segments elliptic, awns parallel' and which can be referred to *S. mucronatum* have been seen, *S. dejectus* being the only species of this group present (Fig. 1). Also on the mica in smaller amounts is *Staurastrum teliferum* and a few semicells which agree quite well with Ralfs' *S. polymorphum* (see Fig. 2e).

The very small *Staurastrum* (fig. 2a-d, f-k) would clearly seem to be the desmid referred to on the packet as *S. paradoxum*, for it has at least a superficial resemblance to the figures which are named as this species by Ralfs (1848, Tab. XXIII, fig. 8a-f). In the latter, however, the processes are much longer and the denticulate ornamentation on them is much more prominent than in the specimens on the mica. The sides of the semi-cell in apical view are straight or convex in the monograph figures, whereas in the herbarium material they are invariably markedly concave. Another significant difference is that in the Ralfs' figures the ventral margins of the semi-cell body are smoothly rounded (obsemicircular to subcyathiform), whereas in the plants on the mica they appear angular due to the presence of a granule, the last of a series, extending on to the semi-cell body from the ventral side of each of the processes (see Fig. 2a and e). Indeed the figures in Ralfs' monograph are very similar to certain planktonic forms of *S. anatinum* in which the body ornament is

very greatly reduced. On the other hand, the desmids on the herbarium mica [illegible] without doubt identical with the small *Staurastrum* which West named *S. micro* (West and West, 1896). The dimensions quoted by Ralfs for his *S. paradoxum* [illegible]

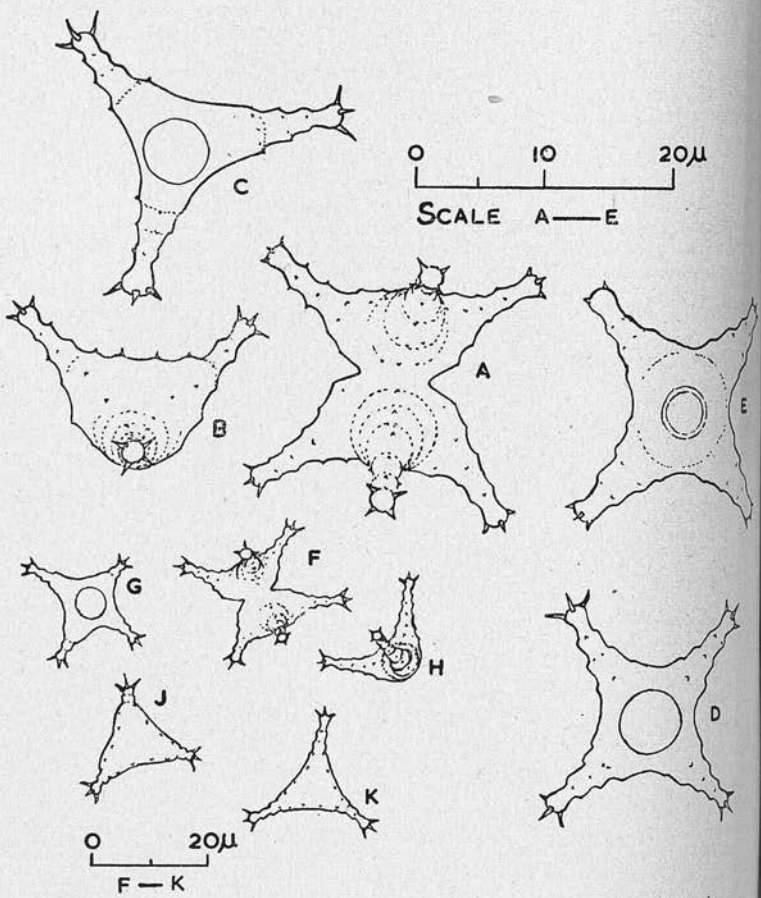


FIG. 2. A—D, F—K, *Staurastrum micron* West 2 E, *S. polymorphum* Breb.

also considerably greater than those of the herbarium material as shown in the following table.

Ralfs *S. paradoxum* 1848, p. 138 (Dimensions quoted originally as fractions of in).		Jenner Herbarium Material		*S. micron* (West and Carter 1923, p. 123)
'l. of frond'	27·9μ	l. sin. pro.	12–15μ	8·5–11·5μ
		l. cum pro.	20–22μ	12·0–17·5μ
'br. of frond'	21·8μ	br. sin. pro.	8–9·5μ	7·0–9·5μ
		br. cum pro	20–23·0μ	12·5–19·0μ
br. isthmus	8·7μ		5.5–6.5μ	3·0–3·5μ
l. processes	18·6–20·2μ		5.0–8·0μ	(5·5–10·5μ) estimated

Since the length of the processes quoted by Ralfs for *S. paradoxum* is between 18·6 and 20·2μ, it would therefore seem reasonable to assume that the total breadth

of the plants depicted in his monograph must have been in the region of 50μ or more, and thus very much larger than *S. micron*. This large size is further evidence in support of the contention that the figures in Ralfs are of a form of *S. anatinum*.

In attempting to find some reason for these discrepancies, it must be admitted that the first impression gained by comparing the general shape and disposition of the processes in the Ralfs' monograph figures with the present drawings (Fig. 2) made from the Jenner Herbarium material is of some measure of similarity. Moreover, another possibly misleading feature is the fact that both triangular and quadrangular individuals have been present in the sample on the mica and both forms are of course depicted in Ralfs' monograph. Thus it must be assumed that Ralfs only looked at this particular material in a cursory manner (see also comments above about *Staurodesmus* (*Staurastrum*) *mucronatus* stated to be on this mica) and unless we are prepared to admit that all of Jenner's drawings and measurements in Ralfs' monograph are much less accurate than is generally supposed (which is not really warranted on other evidence), it can only be assumed that the drawings of *S. paradoxum* in this work were not made from the material now in the British Museum. This anomaly, however, in no way assists in the solution of the problem concerning the identity of *S. paradoxum*. It only seems to provide an additional reason for the adoption of the suggestion that this species should now be abandoned.

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The Published Figures of the Desmid Staurastrum paradoxum

By A. J. BROOK

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■

The original limits of the now very artificial genus *Staurastrum* were based on an imperfect description and two small, enigmatic drawings of a radiate desmid to which MEYEN (1828) gave the name *Staurastrum paradoxum*. It must be admitted, however, that these drawings provide an excellent general characterization of the radiate members of the genus, though it is not possible to concede more than this and relate them, with certainty, to any known desmid. Despite this, many algologists since MEYEN's time have, in the absence of type material, hazarded guesses as to the true identity of *S. paradoxum*. As a result there now exists, scattered throughout the literature, a very considerable number of descriptions and drawings purporting to be of this species. Since it is drawings, rather than descriptions, which are of ultimate importance in confirming the identity of a given desmid, a detailed examination has been made of all of these figures which have been published during the 130 years since MEYEN's description first appeared. The figures examined are listed in Table 1 and reproduced in Figs. 1-62.

Even a cursory examination of the figures shows how vague and variable the concept of *S. paradoxum* has become. In fact it would seem that almost any *Staurastrum* with well developed processes, the body ornamentation of which is greatly reduced or absent, has been referred to *S. paradoxum*. This interpretation of the species has been propounded even by such an eminent algologist as Professor G. M. SMITH who writes (SMITH 1924 a, p. 86), « I have reached the conclusion that the essential characters (of *S. paradoxum*) are the relatively long and divergent processes and an absence of a row of verrucae just within, and parallel to the margin of the cell body in a vertical view of the cell ». In view of the considerable degree of variation in the development of ornamentation (granules, spines and verrucae) which may be apparent in a population of any desmid species, the indefinite character of « absence of verrucae » emphasised in SMITH's description is unfortunate and indeed misleading. Moreover, very many desmid species possess

« relatively long divergent processes », so that even this more positive character, appraised ad diagnostic by SMITH, gives no help in distinguishing *S. paradoxum* from many other species.

Since the establishment of the genus *Staurastrum*, the limits of which were enlarged by RALFS (1848), a very large number of species have been described, especially from the plankton (a habitat certainly not investigated by MEYEN or RALFS), with the more limited characters of the genus as implied in MEYEN's imperfect description of *S. paradoxum*. That is having a small cell body with little or no ornamentation, a well defined median constriction, angular (usually triangular) in end view, and with the angles produced into long, slender, hollow processes. In addition to these general features, these subsequently established radiate species have, however, certain other diagnostic characters by which they can be readily distinguished. Moreover, it will be shown in the following analysis that most of the published figures referred to *S. paradoxum* can be assigned to one or other well defined and adequately described taxon. These figures will now be examined in turn and where possible referred to the *Staurastrum* species to which they most probably belong.

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RALFS (1845, 1848) Figs. 2-6.

The broadly cyathiform semicells, with dorsal margins slightly convex and ventral margins rounded, coupled with the comparatively stout, dentate processes which terminate in three divergent spines, strongly suggest a reduced form of *S. anatinum*. This conclusion is reinforced by the apical view, shown here in Fig. 3, in which there is a row of emarginate granules between each angle of the semicells. The herbarium material, now in the British Museum, from which these drawings are believed to have been made is, however, of *S. micron* (BROOK, 1958 b).

DELPONTE (1878) Figs. 7-8.

The biradiate specimen figures by this author would seem to have affinities with *S. manfeldtii* and in view of the absence of ornamentation on the semicell body is suggestive of a biradiate form of TEILING's *S. planctonicum* (cf. *S. duacense*). However, lateral denticulations on the processes never occur in any species of this group comparable with those indicated in DELPONTE's illustrations.

With regard to the triradiate (?) specimen of DELPONTE (Fig. 8), RALFS' opinions as to the form of *S. paradoxum* have clearly been followed, for this drawing is suggestive of another reduced form of *S. anatinum*.

WOLLE (1884) Fig. 9-10.

These two figures merely indicate the general characters of the radiate members of the genus *Staurastrum* but are not indicative of any particular species, or even species-group, of the genus.

COOKE (1887) Figs. 57-62.

Although COOKE does not appear to acknowledge the fact, it seems clear that his illustrations of *S. paradoxum* are only rather inexact copies of RALFS' (1848) figures of this species (cf. with Figs. 2-6).

NORDSTEDT (1888) Figs. 42-43.

There seems to be little doubt that one of NORDSTEDT's drawings (Fig. 42) is of a form of *S. manfeldtii*, probably near the var. *planctonicum*, while the other (Fig. 43) which he states to be « ad *S. gracile* accedent » is clearly close to TEILING's *S. planctonicum*, the planktonic relative of *S. manfeldtii*.

TURNER (1893) Figs. 44-45.

TURNER's biradiate form (Fig. 45) is suggestive of *S. tetracerum* RALFS, while his triradiate specimen (Fig. 44) would seem to be a form of *S. excavatum* West & West.

COMÈRE (1901) Fig. 38.

It is impossible to interpret the three small sketches which this author refers to *S. paradoxum*. Moreover, there is some error in the scale of these figures which are stated to be × 350 diameters and therefore approximately 24 µ × 30 µ, while the dimensions quoted in the text are 72 µ × 40-60 µ.

WEST and WEST (1905 a) Figs. 11-12.

These authorities have clearly followed RALFS in referring these forms from the plankton of the Orkneys and Shetlands to *S. paradoxum*. There seems to be little doubt that these are in fact forms of *S. anatinum* with short processes and reduced ornamentation.

West and West (1905 b) Figs. 13-15.

As in the earlier paper of these authors, Fig. 15 is another reduced form of *S. anatinum* (cf. Fig. 4). The other specimens illustrated in this paper, however (Figs. 13-14) can only be interpreted as forms of *S. cingulum* in which the isthmal ornament of a ring of granules is absent.

Ostenfeld and Wesenberg-Lund (1906) Fig. 40.

This figure would seem to be yet another planktonic form of *S. anatinum* in which not only is the ornamentation of the semicells reduced but also that of the processes.

Migula (1907-09) Fig. 18.

There seems to be little doubt that Migula's figure is merely a copy of Ralfs' (1848) Fig. 8 a of Tab. 23 (see Fig. 2) in which the ornamentation of the processes has, for some reason, been omitted.

West and Carter (1923) Figs. 11-17.

The figures in this monograph are taken from the previously published papers of West and West (see above West and West 1905 a, 1905 b) with the exception of two (Figs. 16-17) drawn by Dr. Nellie Carter. Fig. 16 is thought to be yet another planktonic form of *S. anatinum*, though Thomasson (1957) believes it to be a form of a species which he has named *S. vulgaris*. His own illustrations of this new species, however, are reminiscent, as he himself admits (p. 252) of certain forms of *S. cingulum* and show little similarity to Dr. Carter's figure.

The other figure drawn by Dr. Carter (Fig. 17) is without doubt another form of *S. cingulum*.

Borge (1923) Fig. 48.

The distinctive ring of isthmal granules, coupled with the general shape of the semicell, points to the conclusion that this *S. paradoxum* of Borge is in fact a form of *S. cingulum* approaching the var. *obesum* Smith.

Geitler L. (1924) Figs. 77-79.

The « seminormal » individual, with long processes (Fig. 77) typical of the planktonic forms from which the abnormal semicells

were derived, is suggestive of *S. chaetoceras* (cf. drawings of *S. chaetoceras* in FLORIN 1957, Fig. 34, 4-6, ad cultura).

SMITH (1924 a) Figs. 19-20, 22-23.

SMITH would seem to have followed the interpretations of WEST and WEST and WEST and CARTER (see above) concerning *S. paradoxum* when dealing with this species in his monograph on desmids from the Wisconsin plankton. Fig. 19 reproduced from this monograph is clearly very similar to Fig. 16, drawn from WEST and CARTER (1923) and which, as stated above, is thought to be a planktonic form of *S. anatinum*. SMITH's other figures (Figs. 20, 22-23) are forms of *S. cingulum*, though the first of these (Fig. 20) strongly resembles the var. *obesum* of this species. It is suggested that this latter desmid has been referred to *S. paradoxum* through combining two characters apparent in the WEST and CARTER (1923) figures referred to this species. Firstly, the shape of the semicells is very similar to the reduced forms of *S. anatinum* which the WEST (see above) named as *S. paradoxum*, while the ornamentation would seem to have been matched with the forms, believed to be of *S. cingulum* to which the WEST also gave the epithet, *paradoxum*.

SMITH (1924 b) Fig. 21.

This dichotypical specimen is without doubt a form of *S. cingulum*, the lower semicell, however, approaches the var. *obesum*, while the upper is nearer the type species.

HOMFELD H. (1929) Fig. 76.

The semicelles depicted as breaking away from the zygospore and referred to *S. paradoxum*, show a vague similarity with the quadriradiate forms of referred to this taxon by RALFS (1848). However, the meagne detail shown in HOMFELD's figure does not assist in establishing their true identity.

TAYLOR (1934) Figs. 24-27.

This author's interpretation of *S. paradoxum* from Newfoundland material is clearly based on WEST and CARTER's (1923) monograph for there seems little doubt that Figs. 24-26 are of quadriradiate forms of *S. anatinum* with reduced ornamentation. The smaller form (Fig. 27) with longer processes is however, more difficult to place, and though it might possibly be a form of *S. cingulum*, the three strongly developed spines which terminate each process is a contrary character.

IRÉNÉE-MARIE (1939) Fig. 34-35.

The two specimens figured by IRÉNÉE MARIE from Canada and assigned to *S. paradoxum* are again considered to be forms of *S. anatinum*, though THOMASSON (1957) refers these figures, incorrectly it is believed, to his *S. vulgare*.

REYNOLDS (1940) Figs. 49-55.

The desmid which this author studied in relation to its variability in Swithland Reservoir, Leicestershire, and referred to as *S. paradoxum* is without doubt *S. chaetoceras* (Schröder) G. M. Smith. This would seem to be confirmed not only by careful scrutiny of REYNOLD's drawings, but also by the fact that as is invariably the case with *S. chaetoceras*, both bi- and tri-radiate forms were produced in the population studied. Moreover, a considerable number of samples examined from this reservoir, which were collected between 1946 and 1949, have been examined and found to contain *S. chaetoceras* while no other *Staurastrum* species which could in any way be confused with REYNOLD's drawings, was present.

LEFÈVRE and BOURRELLY (1941) Figs. 72-75.

The triradiate specimens (Figs. 72, 73 & 75) are strongly suggestive of the fairly common desmid of mesoeutrophic lakes, *S. pingue*, while the biradiate form (Fig. 74) can with certainty be attributed to *S. chaetoceras*.

GRONBLAD (1942) Fig. 41.

This figure is almost certainly a form of *S. cingulum* in which the isthmal ring of granules has been difficult to discern, as is quite common. Indeed, the entire granular ornamentation of the specimen seems to be poorly developed.

PRESCOTT and SCOTT (1942) Fig. 56.

On the basis of the shape of the semicell in the region of the isthmus, it is thought that the desmid figured by these authors is a form of *S. longipes*, though the slightly convex cell apices and the form of the terminal spines of the processes are not quite typical of this species.

LIND and PEARSALL (1945) Figs. 29-33.

TEILING (1947) has commented on some of the figures purporting to be of *S. paradoxum* in this paper on Irish plankton. As stated by

this authority, Fig. 32 is without doubt a specimen of *S. cingulum* var. *obesum;* Fig. 31 would seem to be a small form of the type species, *S. cingulum*, while the other figures of these authors (Figs. 29-31) are of forms of *S. anatinum* with reduced ornamentation, common in the plankton of many Irish loughs (Brook 1958a). Thus these authors, as in the case of many others, would seem to have accepted the interpretation of *S. paradoxum* as given in West and Carter (1923) and Smith (1924).

Hori (1945) Fig. 28.

The small desmid from Japanese material named as *S. paradoxum* is probably a form of *S. excavatum* or possibly of *S. tetracerum*.

Nygaard (1945) Fig. 38.

There is some doubt as to whether the specimen in Nygaard's key to the phytoplankton of Danish lakes and named *S. paradoxum* is a drawing of *S. cingulum*, or of a triradiate form of *S. chaetoceras*. On the whole and especially with regard to the shape of the semicells, it is more suggestive of the latter species.

Frémy and Meslin (1947) Figs. 63-71.

The first group of figures of these authors (Figs. 63-68) are undoubtedly of bi- and tri-radiate specimens of *S. chaetoceras*, a diagnosis which accords with the eutrophic environment from which these desmids were collected.

The larger and more robust specimens (Fig. 69-71), however, are not at all typical of *S. chaetoceras* but would seem to resemble *S. cingulum* var. *obesum*, a taxon which may also occur in eutrophic waters.

Yamagushi and Hirano (1953) Fig. 47.

This would seem to be yet another case of a planktonic form of *S. anatinum*, with typically reduced ornamentation, being referred to as *S. paradoxum*.

Hirano M. (1952 a) Fig. 80.

The fact that both bi-radiate and somewhat smaller triradiate forms of the desmid referred to as *S. paradoxum* by this author were found, confirms the identity of Fig. 80 as being of *S. chaetoceras*.

HIRANO M. (1952 b) Fig. 81.

This is clearly a somewhat larger and more robust form of *S. chaetoceras* than that figured in HIRANO's previous paper (see above).

COSSANDEY (1955) Fig. 37.

This *Staurastrum* from the eutrophic Lac de Bret, Switzerland, is clearly a biradiate form of *S. chaetoceras*.

SKUJA (1956) Figs. 36 and 42.

There is no doubt that the two desmids figured in this paper under the name of *S. paradoxum* are in fact forms of *S. pingue* Teiling.

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DISCUSSION.

The foregoing analysis and Table 2, in which its results are summarized, indicate that the figures in the literature which have been named as *S. paradoxum* can in fact be separated into at least ten well defined, and adequately described taxa. From Table 2 it is clear that the greatest number of authors who have published figures assigned to this ill defined species (35 %), have followed the lead given by RALFS as to the identity of *S. paradoxum*, and appear to have selected forms of *S. anatinum* with reduced ornamentation as representative of the species. Since desmid taxonomy begins in the main with RALFS (1848) it might be argued that this interpretation of the species should be accepted. However, an examination of RALFS' type material of *S. paradoxum* in the Jenner Herbarium of the British Museum (BROOK 1958 b) has shown not reduced forms of *S. anatinum*, as indicated by JENNER's figures in RALFS' (1848) monograph, but the small desmid which WEST and WEST (1896) named *S. micron*. These latter authorities, although publishing *S. anatinum*-like figures as representing *S. paradoxum*, (WEST and WEST 1905 a) introduced at the same time an additional concept of the species when they published two figures which are undoubtedly of *S. cingulum*. Thus in the WEST and CARTER's monograph on the British members of the genus *Staurastrum* (WEST and CARTER (1923)), two distinct species are depicted for *S. paradoxum*. Moreover, SMITH (1924 a), in his monograph on the plankton desmids of the Wisconsin lakes, has perpetuated this unwarranted dual interpretation of the species. Other authors both

before and after the publication of these two notable monographs, have added to the general confusion by publishing other interpretations of *S. paradoxum,* so that now its value as a taxonomic unit, especially in the absence of type material, is nil.

Similar confusion, which is not merely a lack of definition concerning the limits of the species, as is common throughout the plant and animal kingdoms, exists with regard to a considerable number of desmid species, especially of the genus *Staurastrum.* This confusion stems from the fact that the species were originally inadequately described and thus subsequent workers, possibly encouraged by the knowledge that most desmids are in any case rather variable organisms, have merley hazarded, what can only be described as somewhat wild, guesses as to their identity. In addition it seems that the names of some of the most confused taxa may have been instrumental in themselves in producing ambiguity. For example, it is surely inviting to assign any doubtful desmid to the species *S. paradoxum :* or forms with slender processes to *S. gracile :* while the specific name *polymorphum* provides another inviting repisitory for « difficult » forms.

In view of this uncertainty about the identity of *S. paradoxum,* it is clear that reference to this species in the many ecological, physiological and phytogeographical papers in which it is mentioned without a good accompanying illustration, can merely denote that some radiate, non-ornamented *Staurastrum* was observed. A similar lack of certainty as to identity exists in the case of a number of other *Staurastrum* species commonly listed in the literature, a fact which points to the need for a full and careful revision of this genus. Finally, it is proposed that the species *S. paradoxum* should be abandoned, for its retention in the absence of type material, can only lead to further vagueness and confusion.

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The author wishes to express his indebtedness for valuable help afforded in the preparation of this paper to Dr. J. W. G. LUND, and the FRITSCH Collection of Illustrations of Algae, at the Freshwater Biological Association, Windermere.

TABLE I

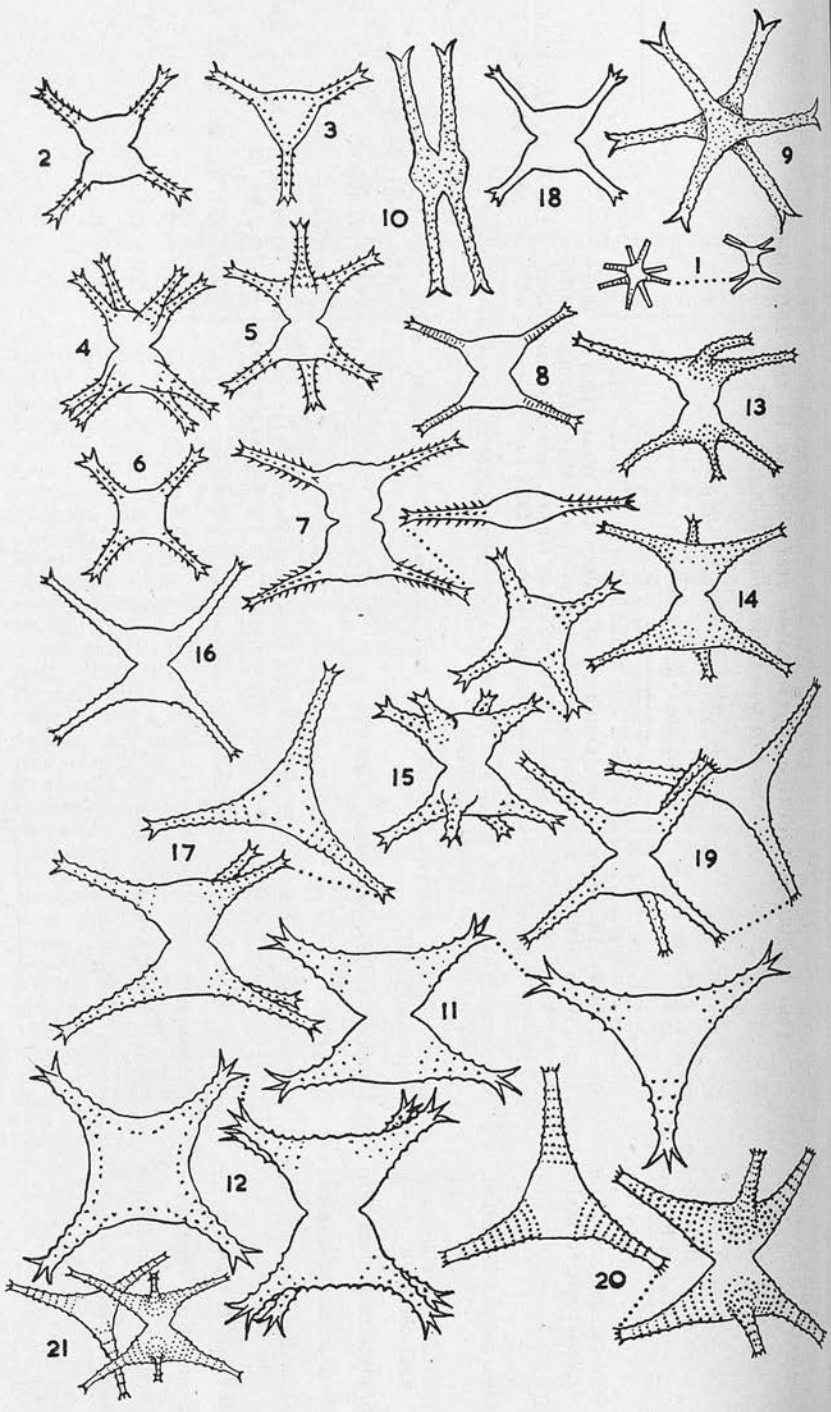
The Published Figures of *Staurastrum paradoxum*

Original Figure Numbers	*Figure in Present Paper.*
Meyen, 1828, Pl. 43, f. 37-38.	Fig. 1.
Ralfs, 1845, Pl. 10, f. 2 a-e.	Figs. 2-6.
Ralfs, 1848, Pl. 23, f. 8.	»
Delponte, 1878, Pl. 11, f. 63-65.	Figs. 7-8.
Wolle, 1884, Pl. 42, f. 36-37.	Figs. 9-10.
Cooke, 1887, Pl. 59, f. 4 a-c.	Figs. 57-62.
Nordstedt, 1888, Pl. 4, f. 10-11.	Figs. 43-44.
Turner, 1893, Pl. 15, f. 4.	Figs. 45-56.
Comère, 1901, Pl. 11, f. 19.	Fig. 38.
West and West, 1903, Pl. 18, f. 4-5.	Figs. 11-12.
West and West, 1905, Pl. 2, f. 33-35.	Figs. 13-15.
Ostenfeld and Wesenburg Lund, 1906, Pl. 25, f. 14.	Fig. 40.
Migula, 1907-09, Pl. 28, f. 3.	Fig. 18.
West and Carter, 1923, Pl. 145, f. 1-5.	Figs. 11-17.
Borge, 1923, Pl. 2, f. 4.	Fig. 48.
Geitler, 1924, f. c & d.	Figs. 77-79.
Smith, 1924 a, Pl. 72, f. 15-22, Pl. 73, f. 1-2.	Figs. 19-20, 22-23.
Smith, 1924 b, Pl. 18, f. 8-9.	Fig. 21.
Homfeld, 1929, L. 80, f. 101.	Fig. 76.
Taylor, 1934, Pl. 17-19.	Figs. 24-27.
Irénée-Marie, 1939, Pl. 48, f. 11-12, Pl. 54, f. 1.	Figs. 34-35.
Reynolds, 1940, Fig. 2 a-g.	Figs. 49-55.
Lefèvre, and Bourrelly, 1941, f. 72-75.	Figs. 72-75.
Gronblad, 1942, Pl. 4, f. 20.	Fig. 41.
Prescott and Scott, 1942, f. 12.	Fig. 56.
Lind and Pearsall, 1945, f. 15-19.	Figs. 29-33.
Hori, 1945, f. St. 2.	Fig. 28.
Nygaard, 1945, Pl. 4, f. 57.	Fig. 38.
Frémy and Meslin, 1947, f. 1-9.	Figs. 63-71.
Hirano, 1952 a, f. 5.	Fig. 80.
Hirano, 1952 b, f. 5.	Fig. 81.
Yamagushi and Hirano, 1953, f. 17.	Fig. 47.
Cossandey, 1955, Pl. 2, f. 14.	Fig. 37.
Skuja, 1956, Pl. 37, f. 15, Pl. 38, f. 1-3.	Figs. 36 and 42.

TABLE II

The Probable Identity of Desmids Referred to in the Literature as *Staurastrum paradoxum*

Taxa Identified from Published Figures	Original Reference		Figure No. in Present Paper	
Staurastrum anatinum (planktonic forms)	Ralfs (1848), Delponte (1878), Cooke (1887), West and West (1905 a), West and West (1905 b), Ostenfeld and Wesenberg-Lund (1906), Migula (1907), West and Carter (1923), Smith (1924 a), Taylor (1934), Irénée-Marie (1939), Lind and Pearsall (1945), Yamagushi and Hirano (1953).	(13)	2-6, 8, 11, 12, 15, 16, 18, 19, 24-26, 29-31, 34-35, 40, 47, 57-62.	(28)
Staurastrum cingulum	West and West (1905), West and Carter (1923), Smith (1924 a), Gronblad (1942), Lind and Pearsall (1945).	(5)	13-14, 17, 22-23, 32, 40, 48.	(8)
Staurastrum cingulum var. *obesum*	Smith (1924 a), Smith (1924 b), Lind and Pearsall (1945), Frémy and Meslin (1947).	(4)	20-21, 33, 69-71.	(6)
Staurastrum manfeldtii	Delponte (1878), Nordstedt (1888).	(2)	7, 43.	(2)
Staurastrum planctonicum	Nordstedt (1888)?	(1)	44.	(1)
Staurastrum chaetoceras	Geitler (1924), Reynolds (1940), Lefèvre and Bourrelly (1941), Nygaard (1945), Frémy and Meslin (1947), Hirano (1952 a & b), Cossandey (1955).	(8)	49-55, 38, 37, 74, 63-68, 77-79, 80, 81.	(19)
Staurastrum pingue	Taylor (1934)?, Skuja (1956), Lefèvre and Bourrelly (1941).	(3)	27?, 36, 42, 72, 73, 75.	(6)
Staurastrum longipes	Prescot and Scott (1942).	(1)	56.	(1)
Staurastrum excavatum	Turner (1893)?, Hori (1945).	(2)	45?, 28.	(2)
Staurastrum tetracerum	Turner (1893)?	(1)	46.	(1)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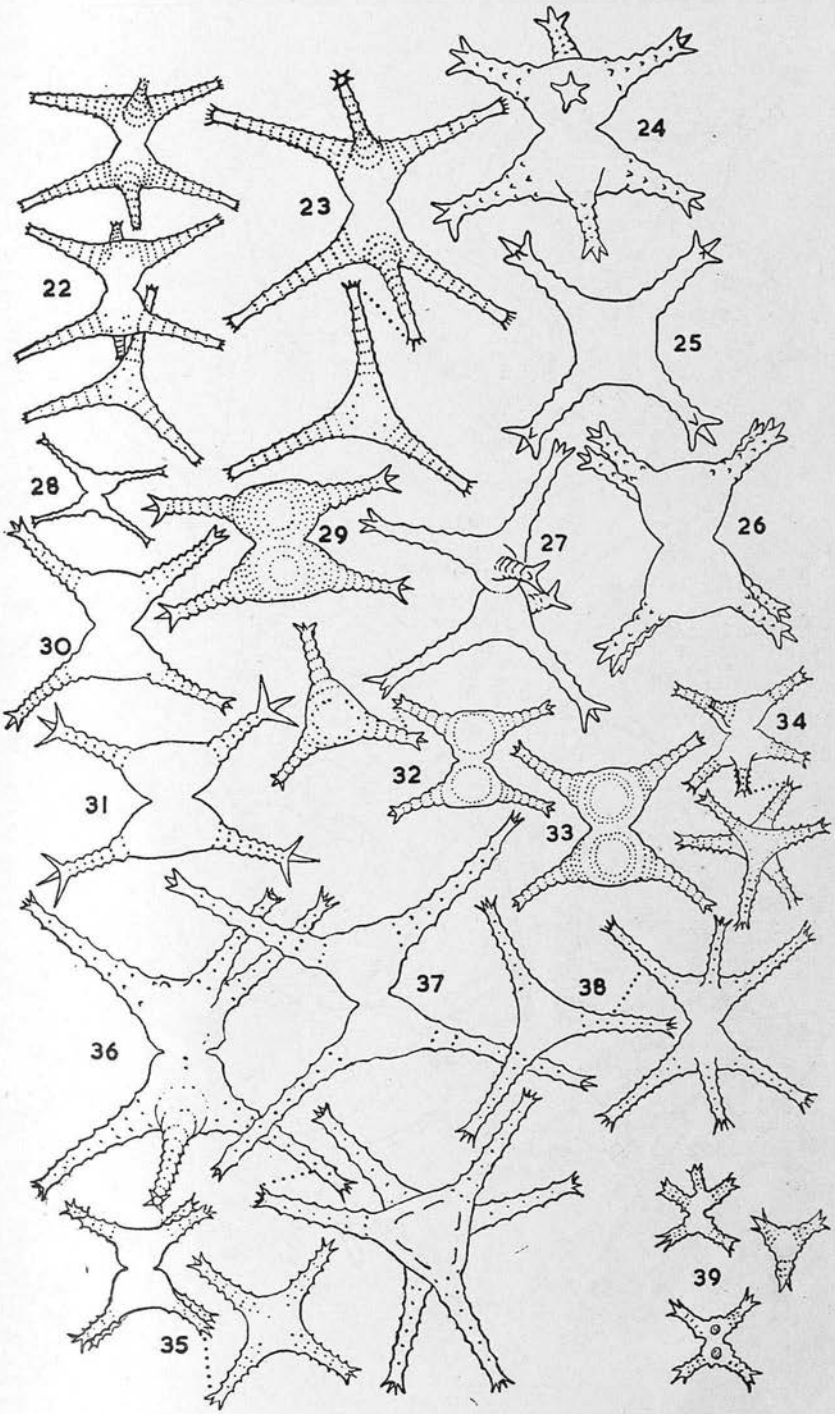
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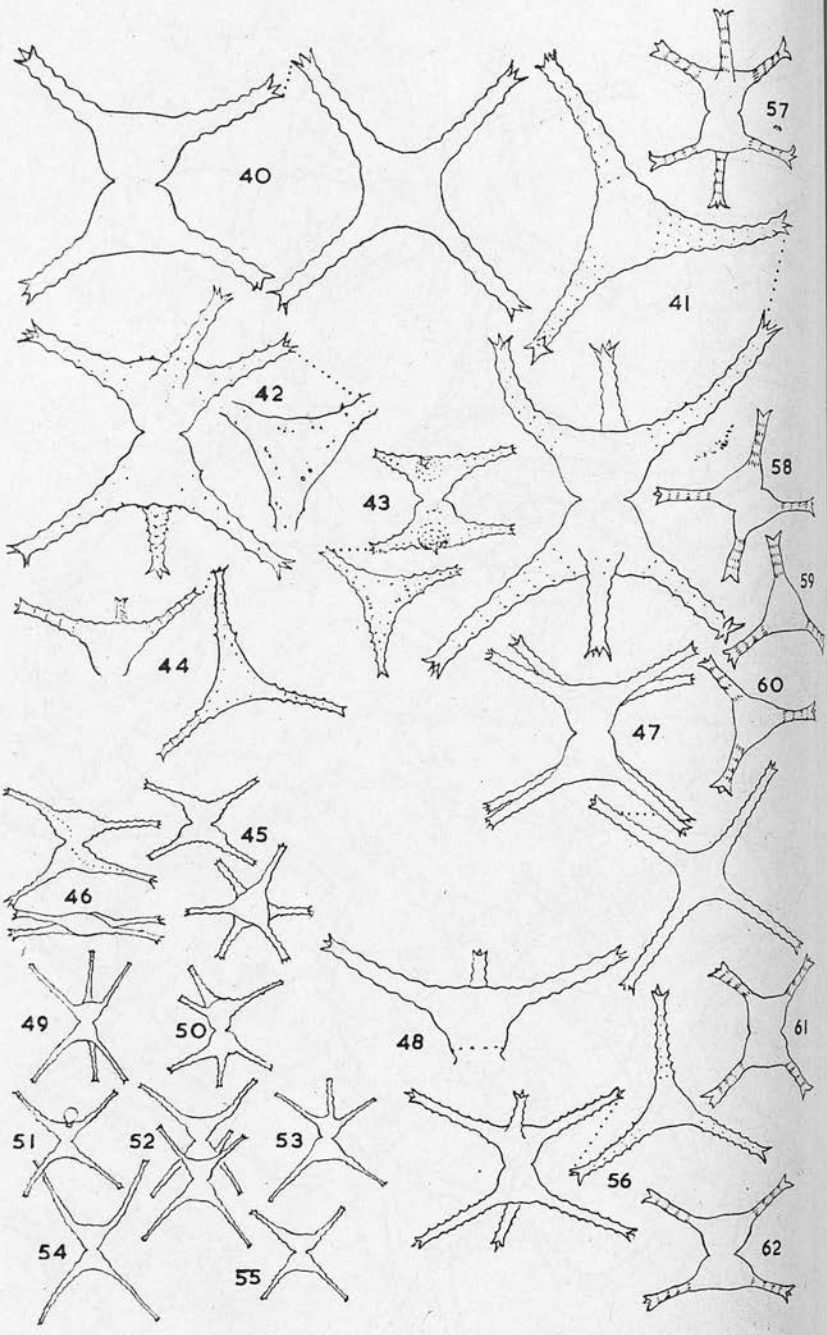
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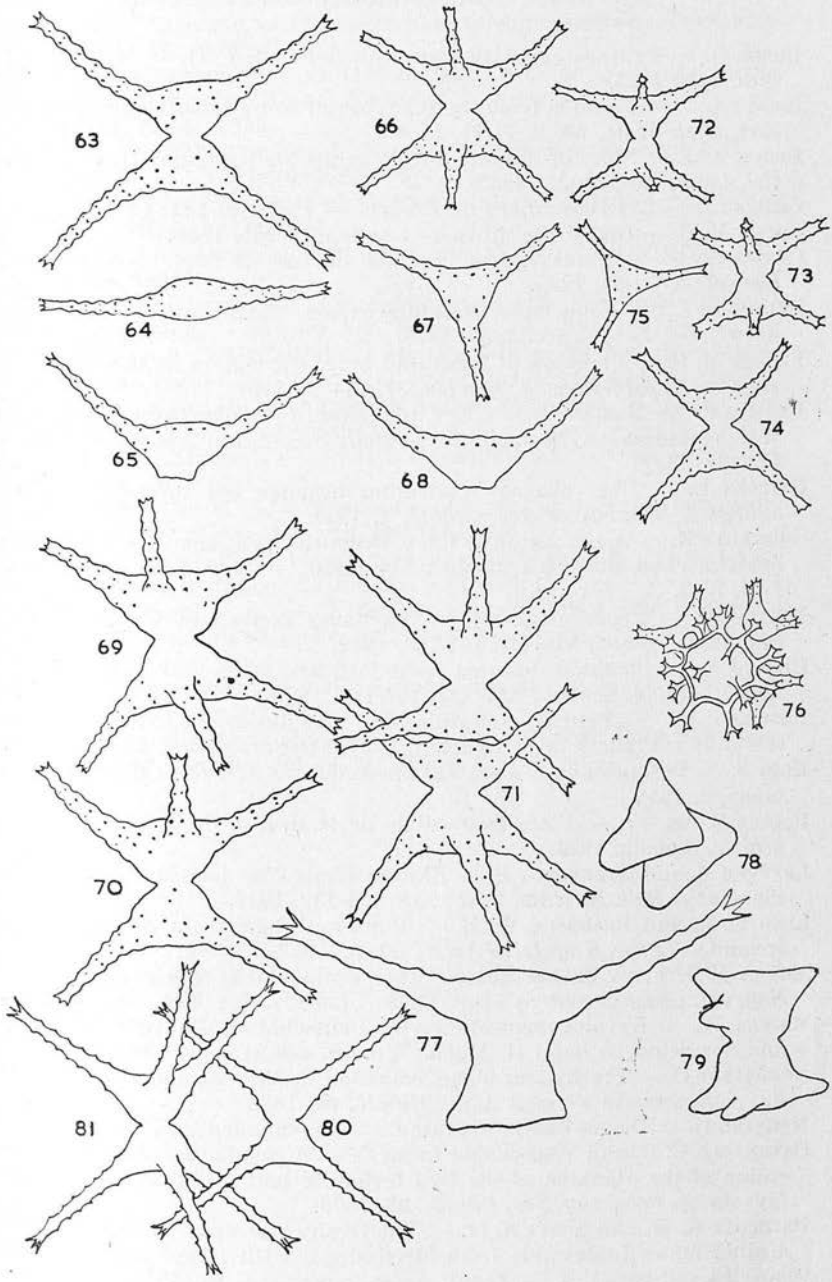
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TRANSACTIONS

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"STAURASTRUM PARADOXUM" MEYEN AND "S. GRAC RALFS IN THE BRITISH FRESHWATER PLANKTON, A REVISION OF THE "S. ANATINUM"-GROUP OF RADIATE DESMIDS

BY

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[WITH EIGHTEEN PLATES AND FOUR TEXT-FIGURES]

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XXVI.—*Staurastrum paradoxum* Meyen and *S. gracile* Ralfs in the British Freshwater Plankton, and a Revision of the *S. anatinum*-group of Radiate Desmids.*

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Communicated by Professor J. R. Matthews, C.B.E. (With Eighteen Plates and Four Text-figures.)

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Synopsis

An attempt has been made to determine the identity of two desmids commonly recorded from the plankton of British lakes, *Staurastrum paradoxum* and *S. gracile*. The original descriptions of these species were clearly inadequate and many subsequent investigators have given their own interpretation as to their identity, so that from the British plankton alone at least six well-defined taxa have been referred to as *S. paradoxum* and four as *S. gracile*. Owing to this confusion, and in the absence of type material, it is suggested that the species *S. paradoxum* cannot be maintained. On the other hand, type material of *S. gracile* exists in the British Museum and has been re-examined. The principal characters of this species are described and figured and a list of synonyms given. In addition, those *Staurastrum* species and varieties frequently misnamed *paradoxum* or *gracile*, have been described in detail.

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1. Introduction

The published records suggest the *Staurastrum paradoxum* Meyen and *S. gracile* Ralfs are the most widely distributed planktonic desmids in British, as well as in other European freshwaters. However, the examination of over 250 plankton samples from all parts of Scotland, from many English lakes, including all the larger Lake District lakes and from a number of loughs in Western Ireland, has shown that none of the *Staurastra* occurring in them can be referred to either species. It has already been suggested (Brook 1959*b*) that the species *paradoxum* cannot be maintained since the published figures so named, and relating not only to British, but to material from many parts of the world, can in most cases be assigned to other clearly defined species. The principal reasons for this confusion would seem to be first, the inadequacy of Meyen's (1828) original description and drawings, and secondly, in the two most extensively used monographs dealing with planktonic species of *Staurastrum* (West and Carter 1923; Smith 1924), several distinct species seem to be figured under this name. Moreover, the questionable proposal that desmid nomenclature should begin with Ralfs (Nordstedt 1906)

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cannot be considered in the case of *S. paradoxum*, for the material named as such in the Jenner Herbarium of the British Museum and believed to have been used in the preparation of Ralfs's (1848) monograph, is of *S. micron* West (Brook 1959*c*) and clearly does not represent the material on which Ralfs's account was based. Thus it cannot be treated as type and *S. paradoxum* must at best be shelved as a "nominum inquirendum" (Silva 1958).

It seems important to emphasize that West and Carter (1923) make no mention of any *Staurastrum* resembling Teiling's very distinctive *S. pingue* and yet this species has been found, often in abundance, in many British lakes (Brook 1958*a*, 1959*a*). It is suggested that this oversight is due to the fact that in size and general proportions some forms of this desmid approach *S. longipes* (Nordst.) Teiling and *S. cingulum* (W. and G. S. West) G. M. Smith. In addition it seems most significant that in many British waters from which *S. paradoxum* has been recorded (West and West 1903, 1905, etc.; Bachmann 1907; Pearsall 1930; Lind and Pearsall 1945), one or more of these three species have been found often in considerable abundance.

Much confusion also exists as to the true identity of *S. gracile* and it is not surprising that several authors have commented on the difficulties of separating it from *S. paradoxum* (*e.g.* Smith 1924; Lind and Pearsall 1945). This must in part arise from the fact that West and Carter's (1923) drawings of these two species show two distinct forms for *paradoxum* and at least four for *S. gracile*. Moreover, it seems that two of these illustrations are almost the same for each species, *i.e.* fig. 2 of Pl. 145 cannot logically be separated from West's drawing of *S. gracile* in Pl. 144, while fig. 3 of the plate representing this species must surely be regarded as identical with the desmid named *S. paradoxum* in fig. 1 of Pl. 145. Teiling (1947) has suggested that fig. 6 of Pl. 144 (see also Smith 1924, fig. 9D) "has little or nothing to do with *S. gracile*" and a careful examination of desmids of similar shape collected from several British lakes supports Teiling's view that its affinities are with the *manfeldti-sebaldi* section of the genus *Staurastrum*: probably a form of *S. planctonicum*. West's fig. 4 of Pl. 144 is suggestive of a small form of this same species (Teiling 1947, fig. 17).

2. An Examination of the Type Material of *S. gracile* Ralfs

Fortunately, in contrast to *S. paradoxum*, type material of *S. gracile* exists in the British Museum and three micas of this, prepared from material collected by Ralfs from Penzance and now in the Jenner Herbarium of the Museum, have been examined. This same material appears to have been studied by Professor G. M. Smith when preparing his monograph on the Wisconsin phytoplankton (Smith 1924, p. 89), but unfortunately in this work the characterization of *S. gracile* seems to have been based primarily on an examination of only vertical views of the plants (see his text-fig. 9A–C), for no side views of the desmid are shown or described.

The present examination of this type material from which the drawings in text-fig. 3 have been prepared, has revealed the following important points:

1. *S. gracile* is almost certainly not a planktonic desmid, the type material having been taken from amongst weeds (*Myriophyllum*) many pieces of which, along with typical weed-living algæ, such as filaments of *Zygnema* sp., *Bulbochæte* sp., and the diatom *Eunotia gracilis*, are present on the micas. Here, it seems, lies the first major source of error in delimiting the species, for most subsequent workers on desmids seem to have tacitly assumed that *S. gracile* is essentially a planktonic species. At best it can only be classed as tychoplanktonic.

2. The type material differs considerably from Jenner's drawings of the species in Ralfs's monograph (Ralfs 1848, Tab. XXII, fig. 12*a–d*). The vertical views in the latter show the margins of the semicells to be distinctly concave, whereas in the herbarium material they are almost straight or even slightly convex (see text-fig. 1 and Smith 1924, text-fig. 9A–C), thus giving the body of the plants a more robust and tumid appearance than Jenner's drawings would suggest. In side view, too, considerable differences are apparent, the cyathiform semicell body being broader and more rounded than in Jenner's fig. 12*a*. The apex in side view is convex instead of being more or less flat, and the processes slightly convergent instead of being parallel. In addition, these processes which seem to be longer and more slender in the illustrations in Ralfs's monograph, appear to be tipped with only three short spines, whereas the processes in the type specimens are all terminated by four short spines. Ralfs states, however (p. 136), in this connection that "Mr Jenner informs me that the processes really terminate in four points which are visible only when a process presents its extremity to the observer".

   Ralfs gives no details concerning the ornamentation of the semicell body, though Jenner's fig. 12*d* ("transverse view") shows an isthmal ring of granules which was also present in all specimens of the type material examined.

3. Many species of *Staurastrum* when observed in vertical view are seen to possess, as does the Jenner Herbarium material of *S. gracile*, an intramarginal row of granules that lie in pairs with a vertical row of granules running down to the cell margin from each granule-pair. Smith (1924, p. 89), incorrectly it is believed, attaches too much importance to this character in his diagnosis of *S. gracile* and as a result would seem to have led many subsequent investigators to name as *S. gracile* quite a number of otherwise distinct desmids (e.g. *S. sebaldi* var. *ornatum*), differing markedly from one another and from the type material, in other important characters of taxonomic value. One very constant character with reference to these granule-pairs (small verrucæ) in the type material of *S. gracile* is that most frequently there are three pairs along each semicell margin as seen in vertical views, nine pairs being visible on each semicell apex. A few specimens may possess five pairs of granules along each margin, one pair always occupying a central position along the margin with an equal number of verrucæ on either side.

4. The size range of *S. gracile* given by Ralfs (converted from his measurement quoted in fractions of an inch) are as follows. Length 33–47 μ, breadth 73–93 μ, breadth of isthmus 8 μ. Measurements made of the type material show the length to vary between 32–36 μ, the breadth without the processes 25 μ and including them 45–60 μ, and the breadth at the isthmus 8–10 μ. Thus the two sets of measurements are in reasonably close agreement, and from them it is clear that *S. gracile* must be regarded as a comparatively small desmid and not a large plankton as seems to be indicated by several authorities.

Scattered throughout the very considerable literature on desmids are many figures, certainly well over fifty, illustrating various authorities' concepts of *S. gracile*. Very few of these, however, correspond at all closely with the type material described and figured here, though many are clearly related forms and when our concepts of the taxonomy of the various groups of radiate species of *Staurastrum* become clearer it should be possible to place many of them into appropriate taxonomic groups even if they cannot be assigned to definite species.

Of these illustrations it would seem that the only authority whose figures representing *S. gracile* correspond at all closely to the type material are those of Nygaard (1949). His fig. 37*a–d*, drawn from specimens from Sortedam II in Denmark, and which show tri-, tetra- and penta-radiate plants, come very close in all respects to the figures presented here from the Jenner Herbarium material. Along with these forms, however, Nygaard (1949, fig. 37*e–g*) depicts plants from other lakes which he also names as *S. gracile*, and which certainly have a somewhat similar body shape and ornamentation to the small forms which agree so well with the type material but which differ in the possession of long, slender, divergent processes. These plants, which should probably be regarded as forms or varieties of *S. gracile*, resemble quite closely certain forms of *S. cingulum*, a truly planktonic species, which together with *S. gracile* would seem to constitute an important natural group of radiate desmids and which hereafter will be referred to as the *gracile*-group of the genus *Staurastrum*.

A further question which now arises is whether other previously described species of *Staurastrum* are identical or at least similar to the type material of *S. gracile*. Most important in this connection is a recent paper by Thomasson (1957) who has investigated in considerable detail a number of *Staurastrum* species from Scandinavian mountain lakes. In this paper there are illustrations of *S. borgeanum* Schmidle (Thomasson 1957, fig. 5*d–f*) which show a remarkable resemblance to the type material of *S. gracile* and it is significant that Thomasson states that *S. borgeanum* is not a truly planktonic desmid. In addition, the size range given for *S. borgeanum* agrees closely with the measurements quoted above for the Jenner Herbarium material. Thomasson has listed in his paper a number of *Staurastrum* taxa which he considers to be synonymous with *S. borgeanum*. Of these, one which shows a very striking similarity with the type material of *S. gracile* is the quadriradiate *S. proboscidium* var. *productum* Messikommer (Messikommer 1942, Pl. XVII, fig. 3) whose size range is also in close agreement.

Clearly, in view of these considerations, the previously accepted but obviously erroneous concept of *S. gracile* as a fairly large planktonic desmid with slender and usually long, divergent processes, must be abandoned. The true *S. gracile* would instead seem to be a comparatively small benthic species with short parallel or convergent processes, which in view of Thomasson's researches, must be considered synonymous with the following taxa:

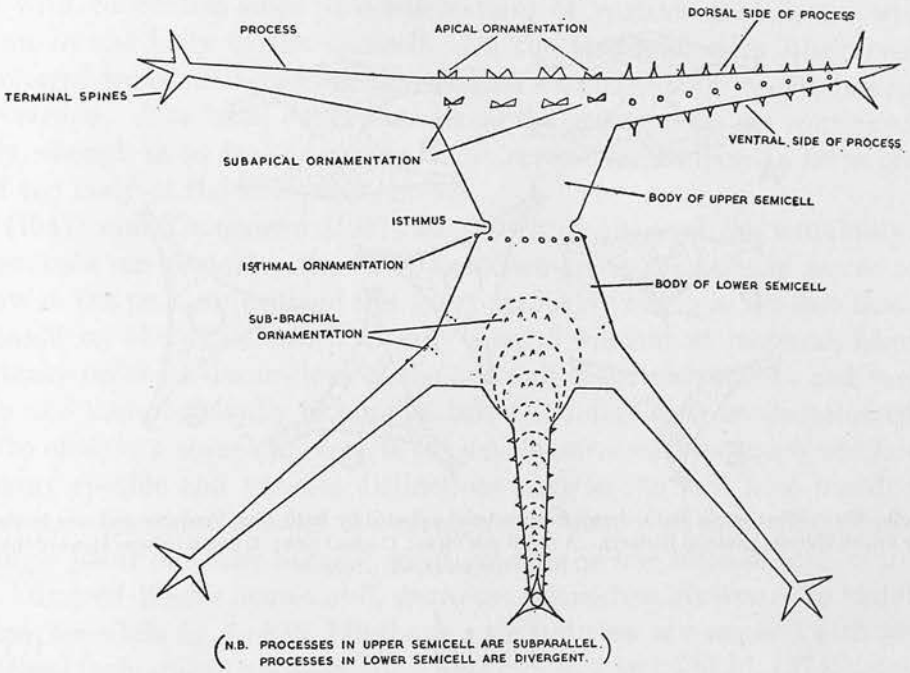
Staurastrum borgeanum Schmidle 1898.
S. hexacerum var. *ornatum* Borge 1894.
S. proboscidium (Breb.) Arch. in Borge 1913.
S. proboscidium var. *productum* Messikommer 1942.
S. borgeanum Schmidle in Gronblad 1926.
S. boreale West and West in Cedercreutz and Gronblad 1936.
S. borgeanum var. *parvum* Messikommer 1949.
S. borgeanum var. *robustum* Messikommer forma in Irenee Marie 1957.

3. A Consideration of those *Staurastrum* Species, and Varieties, frequently named as *S. paradoxum* or *S. gracile*

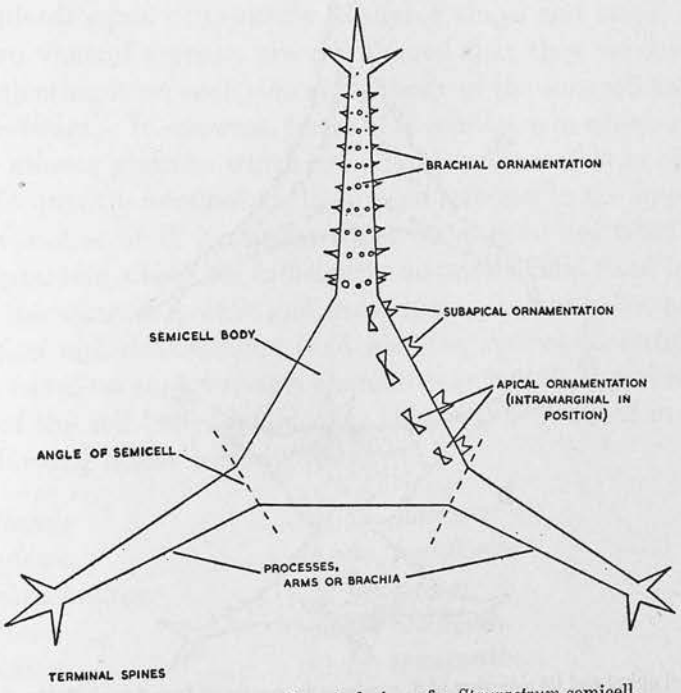
In considering the two confused and confusing species complexes *S. paradoxum* and *S. gracile*, it is clearly important to re-examine in detail the limits of the following more clearly defined species:

(i) *S. anatinum* Cooke and Wills.
(ii) *S. cingulum* (W. and G. S. West) G. M. Smith.

(iii) *S. chætoceras* (Schmidle) G. M. Smith.
(iv) *S. longipes* (Nordst.) Teiling.
(v) *S. pingue* Teiling.



TEXT-FIG. 1.—Diagrammatic side view of a *Staurastrum* plant.

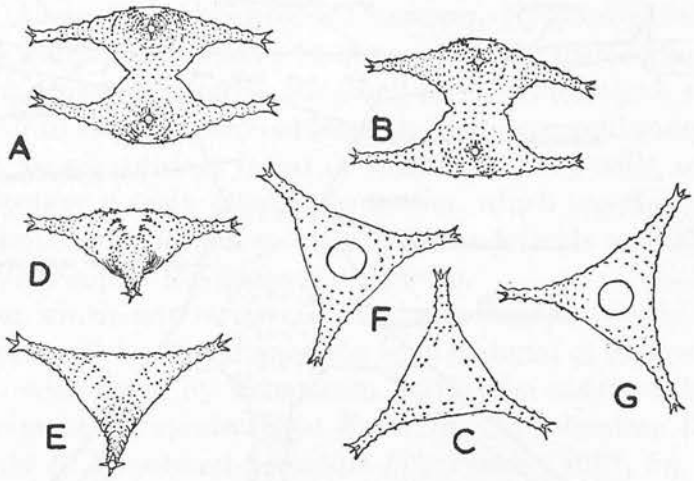


TEXT-FIG. 2.—Diagrammatic apical view of a *Staurastrum* semicell.

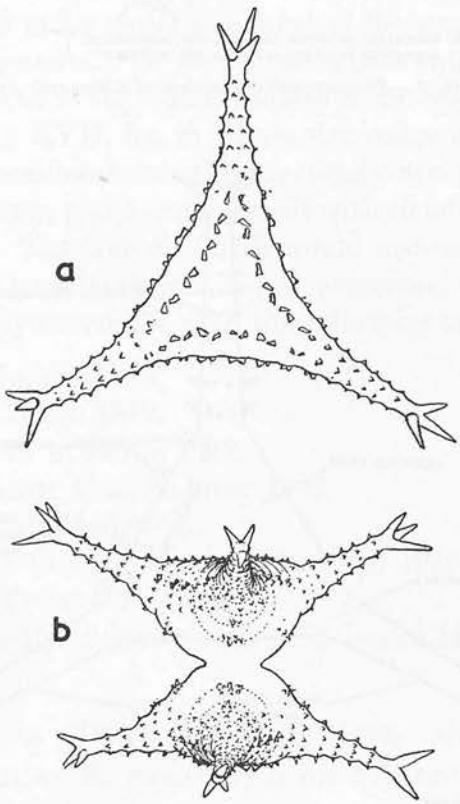
In order to assist in the understanding of the terminology used in the descriptions of the various parts and the ornamentation of the *Staurastrum* species dealt with in the remainder of this paper, annotated diagrammatic figures of apical and side views of a *Staurastrum* are shown in text-figs. 1 and 2.

(i) Staurastrum anatinum *Cooke and Wills*

There are a considerable number of *Staurastrum* species, and their varieties, which possess the basic *anatinum*-shape of semicell. This in its simplest form is well illustrated in figs. 15



TEXT-FIG. 3.—*Staurastrum gracile* Ralfs, drawn from material collected by Ralfs from Penzance and now in the Jenner Herbarium of the British Museum (Natural History). A and B side views; C apical view; D and E oblique views of the apex; F and G transverse views, all ×600.



TEXT-FIG. 4.—(*a*) apical and (*b*) side view of *S. anatinum* fa. *anatinum* from Lough Boffin, Ireland. ×600.

and 16 of Lind and Pearsall (1945) (see also Pls. 1–3) though they have incorrectly called *S. paradoxum*, presumably on the basis of West and Carter's Pl. 145, figs. 1, 3 and 4.

S. anatinum (text-fig. 4) is typified by its subfusiform semicells which are separated by a deeply constricted, acute sinus. Both the ventral and dorsal margins of the semicells are

convex, though the ventral more so than the latter, while the angles are considerably extended to form long, hollow, gradually attenuating processes, which are sub-parallel to divergent and which terminate usually in three stout divergent spines. The processes are provided along their length with concentric rings of denticulations of variable prominence which continue downwards on to the body of the semicell. On the apex and sides (their position here is sometimes referred to as sub-apical) of the semicell six of them are usually much enlarged as emarginate verrucæ. The basal denticulations on the processes do not continue far on to the semicell body, though in so far as they do, they increase in numbers to three granulæ. The remainder of the body of the semicell is smooth.

Teiling (1947) and Thomasson (1957) have both emphasized the mutability of verrucæ, spines and granulæ on desmid cells. The *anatinum*-group of desmids serves to emphasize especially how in the past, students of this group, probably owing to the fact that descriptions have been based on the examination of only a small amount of material, have placed too much importance on these decorations of the cell wall in defining species and varieties. In a given sample and more especially in samples taken at intervals from the same body of water it is possible to observe a complete range in the development of these apical and lateral verrucæ (on which many specific and varietal distinctions have in the past been based) from almost indiscernible single granules to large spines, stout verrucæ, or even doubly bifurcate verrucæ. Even in a single plant one may observe small granules in one semicell and bifurcate verrucæ in the other. Indeed West's figures of *S. anatinum* themselves illustrate the variability of this ornamentation, for while fig. 7 of Pl. 146 shows a ventral view of a semicell with well-developed apical and lateral (sub-apical) verrucæ, the plants in figs. 1 and 5 of Pl. 147 illustrating a small form and the var. *longibrachiatum* respectively, are shown to be without lateral ornamentation. On the other hand, plants again of typically *anatinum* shape and apical ornamentation but in which the middle two ventral verrucæ are so enlarged that they are described as "prominent bifurcate spines" projecting from each side of the body of the semicell have been given specific rank and named *S. vestitum*. In contrast, forms of *S. anatinum* in which all the body decoration has been reduced to minute granulæ which are almost indiscernible in cells containing chloroplasts and are thus frequently overlooked, have been referred to the inevitable *S. paradoxum*.

Of the several varieties of *S. anatinum* which have been described it is not questioned that some possess characters which are sufficiently distinctive and fixed to warrant them being maintained, such as the varieties *grande* and *truncatum*. On the other hand, varieties such as *curtum*, *longibrachiatum* and *denticulatum* (and also the species *S. vestitum* and its var. *subanatinum*) which are based on such variable characters as length of processes and the extent of various decorations of the cell body should, it is believed, be reduced in rank to the status of forms. Thus the following might be recognized:

(*a*) fa. *anatinum*
(*b*) fa. *pelagicum*
(*c*) fa. *longibrachiatum*
(*d*) fa. *curtum*
(*e*) fa. *hirsutum*
(*f*) fa. *denticulatum*
(*g*) fa. *glabrum*
(*h*) fa. *paradoxum*
(*i*) fa. *tortum*
(*j*) fa. *vestitum*
(*k*) fa. *semivestitum*
(*l*) facies *biradiatum*, *quadriradiatum*, etc.

All of the forms listed above are based only on one particular character, so that the forms *longibrachiatum* and *curtum*, for example, refer only to the length of the desmids processes, in contrast to the forms *hirsutum*, *denticulatum* or *glabrum* which are based on the ornamentation of the semicell body. It must be emphasized, moreover, that the characters on which these

forms are founded are in no way discrete, so that many of the plants encountered may possess a number of these characters. Thus an individual which might be referred to as fa. *longibrachiatum* may also have body ornamentation typical of the fa. *paradoxum* (Pl. V, fig. 5), or alternatively of the fa. *vestitum* (Pl. V, fig. 6). It therefore seems reasonable to suggest for this very variable desmid, the adoption of a system of nomenclature which at the infraspecific level involves the use of a combination of two or even three of these form-epithets. For example, an individual of *S. anatinum* with long denticulate processes but with little or no ornamentation on its body should be referred to as *S. anatinum* fa. *longibrachiatum-denticulatum-paradoxum* (Pl. II, figs. 1 and 2). In order to maintain some uniformity in the use of these epithets and, moreover, since the characters to be described below are all of equal importance, it is suggested that they are used in combination in the order set out in the list above; viz. *curtum-glabrum-paradoxum*, rather than *paradoxum-glabrum-curtum* or *glabrum-curtum-paradoxum*. The diagnoses of the various forms which follow, however, refer only to one particular character, which as stated above must be combined in naming the desmid in question.

(*a*) fa. *anatinum* (see above) (text-fig. 4).

(*b*) fa. *pelagicum* (W. and G. S. West) in *Trans. Roy. Irish Acad.*, **32,** 1902, 55) nov. comb. (Pl. I, figs. 3 and 4; Pl. V, fig. 2; Pl. VII, fig. 1).

Semicells relatively longer than in fa. *anatinum* and more cup-shaped; processes may be rather narrower. Forms which can be termed fa. *pelagicum-vestitum* have been found quite frequently in the plankton of Loch Shin, Sutherland (Pl. VII, fig. 1).

(*c*) fa. *longibrachiatum* (W. and G. S. West 1905, in *Trans. Roy. Soc. Edin.*, **41,** 504) nov. comb. (Pl. V, figs. 1–5; Pl. VII, fig. 5; Pl. II, figs. 1 and 2).

Processes longer than twice the diameter of the sinus. All types of ornamentation of the semicell may be found associated with this character, ranging from that of the simple fa. *paradoxum* to the elaborate fa. *vestitum*.

(*d*) fa. *curtum* (G. M. Smith 1924, in *Bull. Univ. Wisc.*, No. 1270, 95) nov. comb. (Pl. II, fig. 6; Pl. VI, figs. 1 and 2; Pl. IX, figs. 6, 8–10).

A form distinguished by its short and relatively stout processes, which must be no longer than the width of the semicell body. West and Carter's figs. 1, 3 and 4 of Pl. 145, and Lind and Pearsall's fig. 15, referred to by these authors as *S. paradoxum*, come near to this form with regard to process length.

(*e*) fa. *hirsutum* A. J. Brook, forma nov. (Pl. III, fig. 7; Pl. VI, fig. 7; Pl. VII, fig. 2; Pl. VIII, figs. 1–6; Pl. IX, figs. 1, 3, 5–10).

Processi orbibus concentricibus denticulationum prominentium ad corpus semicellulæ extendibus præditi.

Processes provided with concentric rings of denticulations of variable prominence, continuing on to the body of the semicell.

(*f*) fa. *denticulatum* (G. M. Smith) 1924, in *Bull. Univ. Wisc.*, No. 1270, 95) nov. comb. (Pl. II, figs. 1–3, 5–8; Pl. IV, figs. 1–5 and 8).

Forms in which the processes are provided with apical, basal and ventral series of denticulations of variable prominence and which continue on to the body of the semicell.

(*g*) fa. *glabrum* A. J. Brook, forma nov. (Pl. I, figs. 1–4 and 7; Pl. II, fig. 4; Pl. III, fig. 4; Pl. V, fig. 2).

Denticulationes processorum valde reducti vel absentes.

Denticulations on the processes greatly reduced or absent.

(*h*) fa. *paradoxum* A. J. Brook, forma nov. (Pl. I, figs. 1–8; Pl. II, figs. 1–8; Pl. III, figs. 1–3; Pl. IX, figs. 1 and 2).

Ornatus corperis semicellulæ valde reductus vel etiam absens.

Ornamentation of the semicell body greatly reduced or absent.

In this form the ornamentation of the semicell body, in contrast to the processes, has been greatly reduced so that it is most difficult to discern in plants possessing chloroplasts. In empty cells, or in which the chlorophyll has faded, this ornamentation can be seen to consist of only very small granulæ (*cf.* West and Carter 1923, Pl. 145, figs. 1, 3 and 4; Lind and Pearsall 1945, figs. 15 and 16; and Irénée Marie 1939, Pl. 48, figs. 11 and 12 and especially Pl. 54, fig. 1).

(*i*) fa. *tortum* A. J. Brook, forma nov. (Pl. IV, fig. 5).

Processi in vertice visi pari modo earundem partium *S. cyrtocero* Brèb. contorti.

Processes in vertical view bent round in one direction as in *S. cyrtocerum* Brèb.

Forms differing considerably in the character of their body ornament and length of processes may possess this character.

(*j*) fa. *vestitum* (Ralfs 1848, in *Brit. Desmid.*, p. 142) nov. comb. (Pl. V, fig. 6; Pl. VII, figs. 1–5; Pl. VIII, figs. 2–6).

Semicells possessing any of the characters outlined above with, in addition, at least two of the sub-apical verrucæ enlarged so that they appear as spines which may be single or bifurcate and projecting from the middle of each side of the semicell.

(*k*) fa. *semivestitum* (West 1892, in *J. Roy. Micro. Soc.*, **12,** 20) nov. comb.

Processes bent round in one direction when semicells are observed in vertical view as in the fa. *tortum* (see above) and with one furcate spine at the base of the convex side of each process.

(*l*) facies *biradiatum* (West 1892, in *J. Linn. Soc. Bot.*, **29,** 185) nov. comb.—also fac. *quadriradiatum, hexaradiatum,* etc. (Pl. IX, figs. 1–10).

In accordance with Teiling's proposals (1950) relating to the nomenclature of those desmid species which exhibit diversity in their radiation, an appropriate "facies-name" should be given to those forms which differ from the typical triradiate condition. The desmid *S. sexcostatum* Brèb. is believed to be a short-armed (fa. *curtum*), hexaradiate form of *S. anatinum* (Pl. IX, fig. 10).

The species *S. aculeatum* (Ehr.) Menengh. is another desmid which must clearly be included in the *anatinum*-group since it is merely a richly ornamented form with the basic *anatinum*-shape and reduced, subparallel processes. Indeed the figures illustrating *S. vestitum* in West and Carter, Pl. 152, figs. 5 and 6, and *S. aculeatum* in Pl. 153, figs. 2, 1, 3 and 4 in that order, seem to illustrate perfectly a successive reduction in the length of the processes, while Skuja's *S. eurycerum* (1949), Grönblad's *S. zoniferum* (Grönblad 1920) and forms illustrated here in Pl. VIII, figs. 1–5, would seem to belong to the beginning of this series, which it is proposed should now be named *S. anatinum* var. *aculeatum.* Similarly there seems to be no valid reason for maintaining *S. controversum* Brèb. as a separate species and it is proposed to rename this *S. anatinum* var. *controversum.* The diagnoses of these varieties are as follows:

S. anatinum var. *aculeatum* ((Ehr.) Menengh. 1840, in Synops. Desm.) nov. comb. (Pl. 8, p. 226, fig. 6)

Cells up to $1\frac{1}{3}$ times broader than long, deeply constricted and with an acute open sinus. Semicells subfusiform to subelliptic and tending to differ from the type species

in that the dorsal and ventral margins are almost equally convex. Angles slightly or not at all produced and terminating in three, or sometimes four, stout divergent spines. When the angles are produced the arms thus formed are usually parallel or slightly convergent and bear a series of denticulations beneath. Apex of semicell with a dorsal series of granulæ, spines or verrucæ, the median one being emarginate, while a lateral series of similar decorations run from angle to angle across the face of the semicell. Ventral view triangular or quadrangular, side nearly straight and angles little produced, tipped with three or four strong spines; lateral margins with a row of granulæ, spines or verrucæ (see *S. vestitum*, Croasdale 1957, Pl. VIII, fig. 119) and with a similar dorsal series just within each lateral margin.

S. anatinum var. *controversum* (Brèb. 1840 in Menegh. Synops. Desm., p. 228) nov. comb.

Cells up to $1\frac{1}{3}$ times broader than long, deeply constricted and with an acute sinus, widening rapidly outwards. Semicells fusiform or subelliptic, lower margin ventricose and dorsal margin strongly convex. Angles produced gradually to form short stout, strongly incurved processes, tipped with three spines and with two or three series of denticulations beneath. Apex of semicells with a dorsal series of granulæ, spines (sometimes bifurcate) or verrucæ, running from angle to angle and with a similar lateral series as well. Vertical view three to five radiate, angles produced into short tapering processes all bent, often abruptly, in one direction (*cf.* fa. *tortum* above), lateral margins concave with a marginal row of spines, granulæ, or verrucæ which may be somewhat displaced by the twisting of the processes.

The affinities of *S. aculeatum*, *S. vestitum* fa. *tortum* and *S. controversum* have previously been commented on by Irénée Marie (1939, p. 326).

The diagnoses of the two remaining varieties of *S. anatinum* which it is proposed to maintain are as follows:

S. anatinum var. *grande* W. and G. S. West (Pl. X, fig. 1)

A very distinctive form which is usually about twice as large in respect of most of its dimensions as the type form (*i.e.* fa. *anatinum*). Ornamentation of the body of the semicells and processes similar but very strongly developed; most frequent difference is that processes are usually tipped with only two spines (see however, Pl. X, fig. 1) which are usually hollow and lying in the same plane one above the other when the semicells are observed in ventral view.

S. anatinum var. *truncatum* West (Pl. X, figs. 2–4)

This is another large variety of *S. anatinum* though not as large as var. *grande*. The semicells are more elliptic than in the type form owing to the fact that the ventral and dorsal margins are more or less equally convex, though the apex itself is distinctly flattened. Processes are short and stout and most frequently appear almost parallel in side view, though forms have been found in which they are as divergent as in the type species. Like the var. *grande* the processes are usually tipped with only two stout hollow spines which, when seen in ventral view, lie one above the other in the same plane. The arrangement of the ornamentation is similar to that in the var. *grande* the denticulations and verrucæ being much more robust than in the type species.

There seems to be no valid reason why the var. *lagerheimii* (Schmidle) W. and G. S. West should be maintained, since this would only seem to be a form of var. *truncatum* with very short processes.

(ii) Staurastrum cingulum (*W. and G. S. West*) *G. M. Smith* (=S. paradoxum *var.* cingulum *W. and G. S. West*) (=S. gracile *in Skuja* 1948). Pls. XI–XIV

Of the planktonic desmids in British freshwaters belonging to the *gracile*-group (see above), the most important is *S. cingulum*. The illustrations of this species in West and Carter (1923, Pl. 145, figs. 9 and 10), which was originally described as the variety *cingulum* of *S. paradoxum*, are misleading in that they represent the juncture of the isthmus with the upper and lower semicells as being distinctly angular or, as shown on the left-hand side of fig. 9, the isthmus tends to be partially enclosed by projections from the adjoining semicells. Having found this species in considerable abundance in the plankton in many English, Scottish and some Irish bodies of freshwater, it has become evident, especially from seasonal collections from Windermere and Loch Lomond, that the shape of this basal region of the semicell adjoining the isthmus is very variable. It ranges in shape from subcylindrical as described by West and West (see also Smith 1924, p. 84) to cuneate or even cup-shaped. This variation is also apparent in samples which have been examined from Loch Shin, the source of West and West's original material. Indeed this range of variability, coupled with the fact that parts of the body ornament and especially the isthmal ring of granules or spines may be minute or almost absent and thus very difficult to make out in cells with chloroplasts, would seem to suggest that West and Carter's drawings, especially of *S. gracile* and possibly of *S. paradoxum* (Pl. 144, fig. 5, and Pl. 145, fig. 2, respectively) represent forms of *S. cingulum* with reduced ornamentation. Lind and Pearsall's figs. 19 and 20 which they have referred to *S. gracile* are clearly of *S. cingulum*.

The processes are not always "gracefully curved upwards" as described by West and Carter (1923, p. 105), the present observations having shown this condition to be exceptional, their disposition being most frequently sub-parallel to divergent. In shape they are usually more robust than the Wests suggest, and their length is somewhat variable. They are decorated with equally spaced rings of small spines or granules and terminate in three to five, though most frequently four, small divergent spines.

The vertical view is triangular, the margins in the central body region being slightly concave to flattened or, in rare cases, slightly convex. As in front view the slender processes attenuate gradually from the body and the ornament consists of successive rings of spines or granules. The ornamentation of the body in vertical view is distinctive, consisting of three pairs of intramarginal granules which appear as small verrucæ in front view, and short rows of single granules running downwards at right angles to these on to the sides of the body. The central region of the apex is devoid of ornament. It has been observed in occasional specimens from Windermere that the central granule-pair on the apex may be enlarged and appear as a very distinctive verruca even when viewed vertically (Pl. XI, fig. 12).

In some of the material from Loch Shin, Sutherland, it has been observed that the semicells may be considerably elongated and inflated at the base just above the isthmus, while there is a double series of isthmal granulæ though the remainder of the decoration of the semicells is quite normal. It is proposed that individuals of this type should be referred to as fa. *annulatum* (Pl. XII, fig. 9).

A *Staurastrum* which is common in the plankton of many British lakes of mesotrophic character is *S. cingulum* var. *obesum* Smith (1922). Pl. XIV, figs. 1 and 7–9. Though it does not appear to have been recorded as such, Lind and Pearsall's fig. 18 which has been referred to *S. paradoxum* is very suggestive of *S. cingulum* var. *obesum*, as pointed out by Teiling (1946, p. 81; and 1947, p. 228). This variety of *S. cingulum* is typified by its consistently larger size and its subfusiform semicells which may in some cases resemble the typical *anatinum*-shape

(*cf.* Pl. VI, fig. 6, with Pl. XIV, fig. 7); hence its reference by Lind and Pearsall to one of West and Carter's forms of *S. paradoxum* (*S. anatinum* fa. *paradoxum* Brook). It has relatively short, stout arms and a more robust decoration of the body and processes. This decoration is identical in its general disposition, as seen in both side and vertical views, with the type species. The biradiate facies *Thunmarkii* Teil. has not been found in the British plankton.

A short, slender-armed form but with a distinctly tumid body and thus closely allied to the var. *obesum* has been found to be quite common in Lochs Chalium, Scye and Shurrery, Caithness (Pl. XIV, fig. 2). An examination of other material collected in the summer of 1903 during the Bathymetrical Survey of the Scottish Freshwater Lochs and kindly placed at my disposal by Dr A. C. Stephen, Keeper of Natural History at the Royal Scottish Museum, Edinburgh, has shown this same form to be present in a number of lochs in the Shetland Islands (Pl. XIV, figs. 3–6). These include Lochs Grasswater, Clingswater, the Loch of Collaster, the Loch of Girlista and Punds Water. A comparison of this desmid with the *Staurastrum* which W. and G. S. West (1905) found in these islands and named *S. affine*, clearly indicates that they are identical, though their illustrations showing the arrangement of the granulæ in the apex of this desmid is quite atypical. In order to show its undoubted relationship with the *cingulum*-group it is proposed to reduce this species to a variety and call it *S. cingulum* var. *affine* (West 1905 in *Trans. Bot. Soc. Edin.*, **23**, 26) nov. comb. *S. affiniforme* Grönblad (1920) is probably a quadriradiate form (facies) of this variety. A more or less complete series of forms, many of which are connected by dichotypical individuals can be constructed, starting with *S. gracile* (Pl. XI, figs. 1–4), through forms which are intermediate in character between *S. gracile* and *S. cingulum* (Pl. XI, figs. 5–9), to the slender, long-armed *S. cingulum* and its vars. *obesum* and *affine* (Pl. XI, figs. 6, 8, 13 and 14; Pl. XIII, figs. 1–4).

Also belonging to the *gracile*-group is the smaller *S. boreale* W. and G. S. West. It can be seen from Pl. XIII, figs. 9–13, that the general character of the body of these plants is very similar to that of *S. cingulum*, the most obvious difference being the former's much shorter processes. A less immediately obvious, but very constant difference, however, is the ornamentation of the body of its semicells. Like *S. gracile* and its allies, each side of the apex in vertical view bears three pairs of intramarginal granules (Pl. XIII, figs. 10*a* and 16*a*), but only from the central granule pair of each group of three does a vertical row of granules run down on to the body of the semicell (Pl. XIII, figs. 14 and 16). The other two granule pairs on either side would seem to be only part of the innermost ring of granules which encircle the processes (cf. *S. chætoceras*, Pl. XV). Forms with very much longer, sub-parallel or slightly divergent processes, but bearing this same ornamentation and possessing a similar body shape have been found in moderate abundance in the plankton of a number of Scottish lochs, especially in the Orkney and Shetland Islands (Pl. XIII, figs. 14–16). It is proposed to name these truly planktonic forms in contrast to the short-processed tychoplanktonic species, *S. boreale* var. *planctonicum* var. nov.

(iii) Staurastrum chætoceras (*Schröd.*) *G. M. Smith* (=S. paradoxum *var.* chætoceras *Schröder*). *Pl. XV*

This species is another small-bodied *Staurastrum*, triradiate forms of which could possibly be confused with *S. longipes*, or in certain cases, when the processes are considerably reduced in length (Pl. XV, figs. 1 and 2), with *S. cingulum*. The semicells range in shape from obversely triangular, with ventral margins sublinear (Pl. XV, figs. 4 and 5) to shallow and cup-shaped (Pl. XV, figs. 3 and 6). The angles of the semicells are continued into long, divergent, almost

straight and very slender processes, the angle of divergence on occasions (Pl. XV, figs. 4 and 5, upper semicell; also Smith 1924, p. 99) being a continuation of the angle of the sinus. The processes are slightly attenuated and may become no more than 2 μ broad at their extremities. They are ornamented by transverse, concentric rings of minute granules and terminate in four, very small, divergent spines. The apex of the semicells is flat and in side view its ornamentation, which is most easily seen in biradiate forms consists of three equally spaced apical granules, or small verrucæ (Pl. XV, figs. 4*a* and *b*, 3, 5 and 6). Running down from each central granule or verruca on to the semicell body is a short row of small granules, while from those on either side, there extends a ring of granulæ concentric with those which decorate the processes and encircling the body where it is joined by the processes: cf. *S. boreale*. In many specimens there is a transverse row of minute granules encircling each semicell just above the isthmus as in the *Staurastrum* species of the *gracile* group. In vertical view the body of the biradiate forms appears narrowly elliptic, or in the case of the triradiate forms, triangular with slightly convex sides.

The figures in Plate XV indicate that this species varies considerably in the size of its body, in the length and thickness of the processes, which may be from 20–80 μ long and 2–5 μ broad, and also in the prominence of the ornamentation which at times may be difficult to discern. Teiling (1950, p. 317 and fig. 23) records that the processes of *S. chætoceras* are about half as long in the triradiate semicells of Janus-forms as in the biradiate semicells.

The desmid referred to as *S. tetracerum* var. *validum* W. and G. S. West by Nygaard (1945, fig. 59) is without doubt a short-armed form of *S. chætoceras*, as are also the specimens to which Smith (1924, Pl. 76, figs. 9 and 10) puts the same name, while Nygaard's *S. paradoxum* (Nygaard 1945, fig. 57) is clearly a triradiate form of this species. Also Griffiths's (1925) *S. paradoxum* var. *biradiatum*, which he described and figured from lakes in Shropshire, Cheshire and Staffordshire, and later (1926*a*) from the plankton of several Anglesey lakes as well as from some of the Norfolk Broads (1926*b*), is unquestionably the biradiate form of *S. chætoceras*.

Reynolds (1940) has studied in Swithland Reservoir, Leicestershire, the seasonal differences in the abundance of bi- and tri-radiate forms of a *Staurastrum* to which he has given the inevitable specific name, *paradoxum*. However, his drawings of these plants, coupled with the fact that he was studying a desmid which showed frequent variation in its radiation, is strongly suggestive of the fact that he too was dealing with short processed-forms of *S. chætoceras*. Moreover, plankton samples collected by F. J. Taylor from this reservoir in 1946, and examined during the present investigation have shown *S. chætoceras* to be abundant at times (Pl. XV, figs. 3 and 6).

(iv) S. longipes (*Nordst.*) *Teiling* (1946) (=S. paradoxum *var.* longipes *Nordst.*). *Pl. XVI*, figs. 1–7

It seems that Lind and Pearsall (1945) were the first to suggest that this desmid should be given specific rank instead of being regarded as a variety of *S. paradoxum*. An examination of plankton from some of the Irish loughs on which their suggestion was based indicates, as stated already, that they were confusing this desmid with *S. pingue* Teiling (see p. 602), and it is emphasized again that their fig. 22 resembles the latter species much more closely than *S. longipes*. This error on their part would then explain the rather puzzling and quite erroneous statement on p. 317 that "its semicells resemble *S. gracile*", as indeed their figure does. This presumably refers to their *S. gracile* in figs. 19 and 20 and which as suggested above (p. 599) are forms of *S. cingulum*. The sinus of their *S. longipes* is relatively deep and broad while the

semicells are subcylindrical in shape. In actual fact, however, the sinus of *S. longipes* is acute and shallow and the semicells cuneate or cup-shaped (Pl. XVI, figs. 1–7) as can be seen from the excellent illustrations in West and Carter, Pl. 146, figs. 2 and 3, or in Smith, Pl. 73, figs. 3–6.

The apices of the semicells are flat or slightly concave and the cell body is devoid of ornamentation, this being restricted to granules or spines on the crenulate margins of the long, slender, divergent processes which terminate in four divergent spines.

Quadriradiate forms of this species are quite common in the plankton of many British waters (Pl. XVI, fig. 4) and a 4+5 Janus-form has been found in Loch Shurrery, Caithness (Pl. XVI, fig. 3).

Teiling (1946, p. 81 and fig. 5) has described a var. *contractum* of *S. longipes* in which the body is much shorter and broader than the type, a condition which has the effect of making the sinus more acute. Forms approaching this variety have been observed in the plankton of several Scottish lochs, one especially interesting form with very irregularly crenulate processes (*cf.* the aberrant form of this species from Lough Ballynahinch, W. Ireland, Pl. XVI, fig. 7) having been found in fair abundance in Loch Allan, Morayshire (Pl. XVI, figs. 5 and 6).

(v) S. pingue *Teiling* (1942). *Pls. XVII and XVIII*

Superficially *S. pingue* resembles *S. longipes* and some forms of *S. cingulum* for all three species tend to be of similar dimensions and general proportions, being small-bodied with long, slender, divergent processes. *S. pingue*, however, is quite distinctive in the shape of the basal portion of its semicells and in its apical ornamentation. In front view, the lower part of the semicell is subcylindrical and considering the plant body as a whole the sinus may be said to appear as a broad V-shaped notch in a cylinder. Occasionally a group of three faint granulæ, two below and one above, can be seen just above the isthmus and beneath each process. The apex is essentially flat though it often appears undulate in side view owing to the distinctive apical ornamentation which consists of three pairs of intramarginal swellings surmounted by either one or two small granules, or a single stout spine or prominent verruca. These in vertical view appear as intramarginal granulæ pairs or single spines. Granulæ, spines and verrucæ may be present together on a given apex, which makes the validity of Nygaard's var. *tridentata* doubtful (1949, p. 161, fig. 53) for forms identical with this in their decoration and in the twisting of adjacent semicells (a common characteristic of this species) have been observed in many British plankton collections (Pl. XVII, figs. 1*a*, 3 and 4).

The long slender processes which end in four divergent spines of *S. pingue* are crenulate and a double apical and single ventral row of spines or granules decorate them along their length. When viewed from below it becomes apparent that the triangular shape of the semicell continues down the body to just above the isthmus, the three granules on the inner faces of which can sometimes be observed. Where the processes join the body, three small granulæ can also be observed, especially in cells without cell contents.

Forms somewhat larger than type and thus approaching Teiling's *S. planctonicum* are quite common in the summer plankton of several eutrophic Scottish lowland lochs (Pl. XVIII, figs. 12–14) while a form with conspicuous decoration of the isthmal angles and beneath the processes occurs in Bassenthwaite and may possibly be referred to *S. leutkemuelleri* Donat (Teiling 1947, fig. 9 and Pl. 18, fig. 11).

It should be noted here that one of the forms of *Staurastrum* which Skuja has referred to as *S. paradoxum* in his recent monograph on Swedish phytoplankton (Skuja 1956, Tef. XXXVII, fig. 15, and Tef. XXXVIII, figs. 1–3) is undoubtedly a form of *S. pingue*. Very similar forms have been observed in plankton from Saddington Reservoir, Leicester.

A very careful re-examination has been made of the original plankton samples from a number of lochs in the Shetlands, collected during the course of the Bathymetric Survey (p. 600), to try to determine the exact form of the desmid named *S. paradoxum* var. *evolutum* by W. and G. S. West and recorded by them as being frequent in the freshwater plankton of this island group. However, no *Staurastrum* could be found in any of these samples to correspond exactly with their description and illustrations of this variety, but it seems significant that *S. pingue* was present in eight out of nine of the lochs examined and in fact is quite common in some (*e.g.* Loch of Girlista) (Pl. XVII, figs. 6 and 7). Both *S. paradoxum* var. *evolutum* as described and figured by West and West and Teiling's *S. pingue* are small-bodied desmids with long, slender, and usually divergent, processes. In addition there are two comments concerning the former in West and Carter (p. 107) which help to confirm its identity with *S. pingue.* Firstly it is stated "that the length of the processes is subject to considerable variation", which is very true of the latter, and secondly and more significant "the cells are invariably twisted so that the angles of the one semicell alternate with those of the other". This latter is a very frequent characteristic of *S. pingue* and in no other *Staurastrum* in the Shetland plankton is there any comparable twisting of the semicells. Against these two characteristics must be set the fact that the dimensions for *S. paradoxum* var. *evolutum* given in West and Carter (1923) are considerably smaller than those of typical specimens of *S. pingue* or for any found in the Scottish Lake Survey Samples which have been examined. The length of the latter plants, without processes, is usually between 25–30 μ, whereas in *S. paradoxum* var. *evolutum* it is stated to be 10–11 μ; with processes the length of the former is from 40 to 45 μ while the latter is quoted as being between 27–40 μ. The breadth of the body of each is more nearly comparable being 8–11 μ in *S. pingue* and 7·5–9·5 μ in *S. paradoxum* var. *evolutum,* though the isthmus is proportionately somewhat broader in the former being 6·5–7·5 μ as against 4·5 μ. A further contrary character is the shape of the body in vertical view the sides of *S. paradoxum* var. *evolutum* being described as "distinctly convex". In *S. pingue* they could only be described as slightly convex. Moreover, no apical ornamentation is shown or mentioned for *S. paradoxum* var. *evolutum.* However, since this can be easily overlooked in specimens of *S. pingue* in which the cell contents are still present, no great weight can be attached to this point. On balance, and despite the differences in dimensions quoted above, it is believed that the West's inadequately described *S. paradoxum* var. *evolutum* is probably Teiling's *S. pingue.*

A number of small forms of *S. pingue,* with considerably reduced processes, have been found in the plankton of a number of British lakes and especially in fairly eutrophic water-storage reservoirs. These forms are clearly closely related to if not identical with the small species *S. crenulatum* (Nag.) Delp. (Pl. XVIII, figs. 1 and 2) with which they can be connected to *S. pingue* itself by a series of intermediate types with increasingly larger processes and larger bodies until forms near Teiling's *S. planctonicum* are reached (Pl. XVIII, figs. 4–14).

4. Discussion

It has been stated by Teiling (1947) that the present taxonomy of desmids is for the most part merely a stocktaking and denominating of collected material, quite unfounded on genetic facts. Furthermore, Fritsch (1953) has emphasized the extent of the enormous mass of unrelated data which have been accumulated concerning these unicellular plants and has pointed out that their classification is greatly complicated by the frequent occurrence of intermediate forms between species and even genera. Added to this, there has in many cases

been an over-exaggeration of the importance of minor detail both with regard to cell shape, such as the length and disposition of processes, and cell ornamentation, especially in the degree of development of spines, etc. This has inevitably led to the description of large numbers of species and varieties differing often in only the smallest detail from those already well established, while in fact there is considerable evidence to suggest that many of the characters so emphasized show no marked degree of constancy. This latter fact is especially marked with regard to the *anatinum*-group of *Staurastrum* (see *S. anatinum* from Loch Kinardochy, Pl. IV).

Unfortunately there seems to have been yet another shortcoming on the part of several workers on this algal group and this has led to the principal cause of confusion which an attempt has been made to resolve in the present paper. There has been a tendency to assume that almost any radiate *Staurastrum* with well-developed processes and in which the apical and sub-apical ornamentation is more or less undiscernible, must be *S. paradoxum* or a variety of this species. Careful examination of such forms has in fact shown that with the exception of the distinctive desmid previously called *S. paradoxum* var. *longipes* but now recognized as a separate species, *S. longipes*, and which is truly without decoration on apex or semicell body, all these forms can be placed in one of six good species or varieties. Moreover, apart from distinctive differences in cell shape, the basic arrangement of the ornamentation is in all cases constant and therefore an important specific character which must be examined carefully. Thus the British species of *Staurastrum* to which the name *S. paradoxum*, or some variety of this species have been given are as follows:

1. *S. anatinum* fa. *paradoxum* Brook fa. nov. (=*S. paradoxum* Meyen in West and Carter 1923, Pl. 145, figs. 1, 3 and 4).
2. *S. cingulum* (West and West) G. M. Smith (=*S. paradoxum* var. *cingulum* West and West).
3. *S. cingulum* var. *obesum* G. M. Smith (=*S. paradoxum* Meyen in Lind and Pearsall 1945, fig. 18).
4. *S. pingue* Teiling (possibly=*S. paradoxum* var. *evolutum* West).
5. *S. longipes* (Nordst.) Teiling (=*S. paradoxum* var. *longipes* Nordst.).
6. *S. chœtoceras* (Schröd.) G. M. Smith (=*S. paradoxum* var. *chœtoceras* Schröd., *S. paradoxum* in Reynolds 1940, and *S. paradoxum* var. *biradiatum* Griffiths).

Similar confusion exists in the case of *S. gracile*, and the following clearly defined species have been referred to in the literature as this species:

1. *S. anatinum* fa. *paradoxum* Brook fa. nov. (=*S. gracile* Ralfs in West and Carter 1923, Pl. 144, fig. 3).
2. *S. cingulum* (West and West) G. M. Smith (=*S. gracile* in West and Carter 1923, Pl. 144, fig. 5).
3. *S. sebaldi* var. *ornatum* fa. *planctonicum* Teiling (=*S. gracile* in Worthington and Macan 1951, Pl. XX).
4. *S. planctonicum* Teiling (=*S. gracile* forma in West and Carter 1923, Pl. 144, fig. 6).

From an ecological standpoint, the separation of the above taxa from the two ill-defined species complexes *S. paradoxum* and *S. gracile* is most important, for it has been found (unpublished data) that most of these taxa seem to be constantly associated with certain types of lakes. In the past, however, *S. paradoxum* and, to a lesser extent, *S. gracile* seem to have been regarded as cosmopolitan species occurring, often in abundance, throughout the trophic range. Baldi's belief (1946) that "the often emphasized cosmopolitanism of freshwater

species . . . constitutes only an appearance which masks the more subtle fragmentation of species into minor units", might in the present case be modified to read, "the often emphasized cosmopolitanism of freshwater species constitutes only an appearance masked by the indiscriminate grouping of distinctive taxonomic units into a single species"! The ecological aspects of the present study, which will be published later, will it is hoped, confirm this latter statement.

5. Summary

1. Resulting from the examination of a large number of phytoplankton samples from lakes of various types in many parts of the British Isles, it has been found that none of the desmids occurring can properly be referred either to *Staurastrum paradoxum* Meyen or to *S. gracile* Ralfs, though these two taxa appear in nearly all previously published systematic lists of British phytoplankton.

2. It is proposed that the ill-defined species *S. paradoxum* should be abandoned since no type material exists from which its true identity could be established.

3. Ralfs's material of *S. gracile* from the Jenner Herbarium of the British Museum has been examined and from it the main characteristics of this species are described. Other species clearly synonymous with *S. gracile* are listed.

4. Those *Staurastrum* species and varieties which seem to have been most frequently named either as *S. paradoxum* or *S. gracile* are considered in detail. These are *S. anatinum*, a very variable species, the taxonomy of which has been revised; *S. cingulum*, a species closely related to the authentic *S. gracile*; and *S. chætoceras*, *S. longipes* and *S. pingue*.

5. Some of the factors probably responsible for the confusion which has arisen concerning the identity of these radiate *Staurastrum* species are discussed.

6. Acknowledgments

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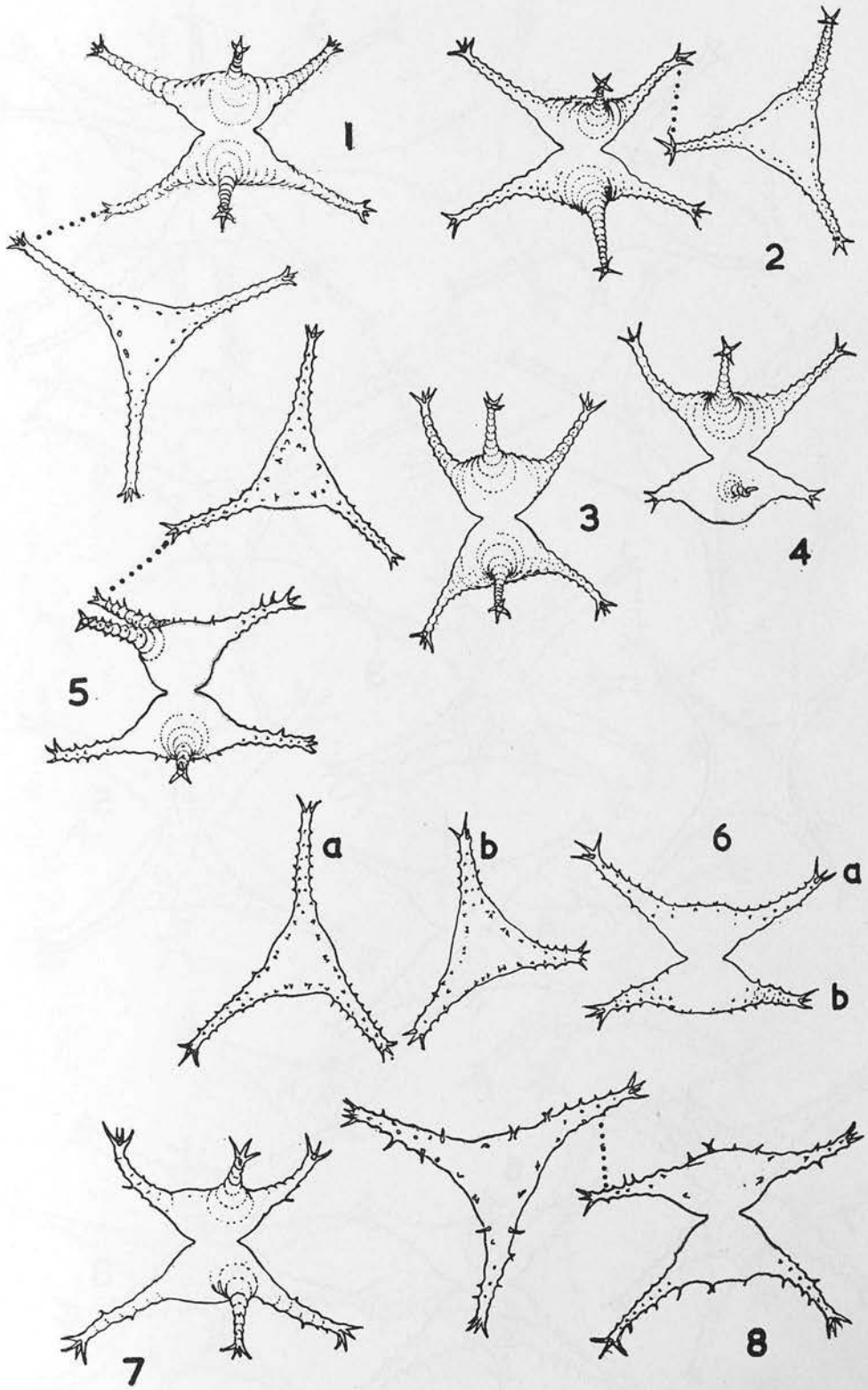
A. J. BROOK, "*Staurastrum paradoxum* Meyen and *S. gracile* Ralfs in the British Freshwater Plankton, and a Revision of the *S. anatinum*-group of Radiate Desmids".—PLATE I.



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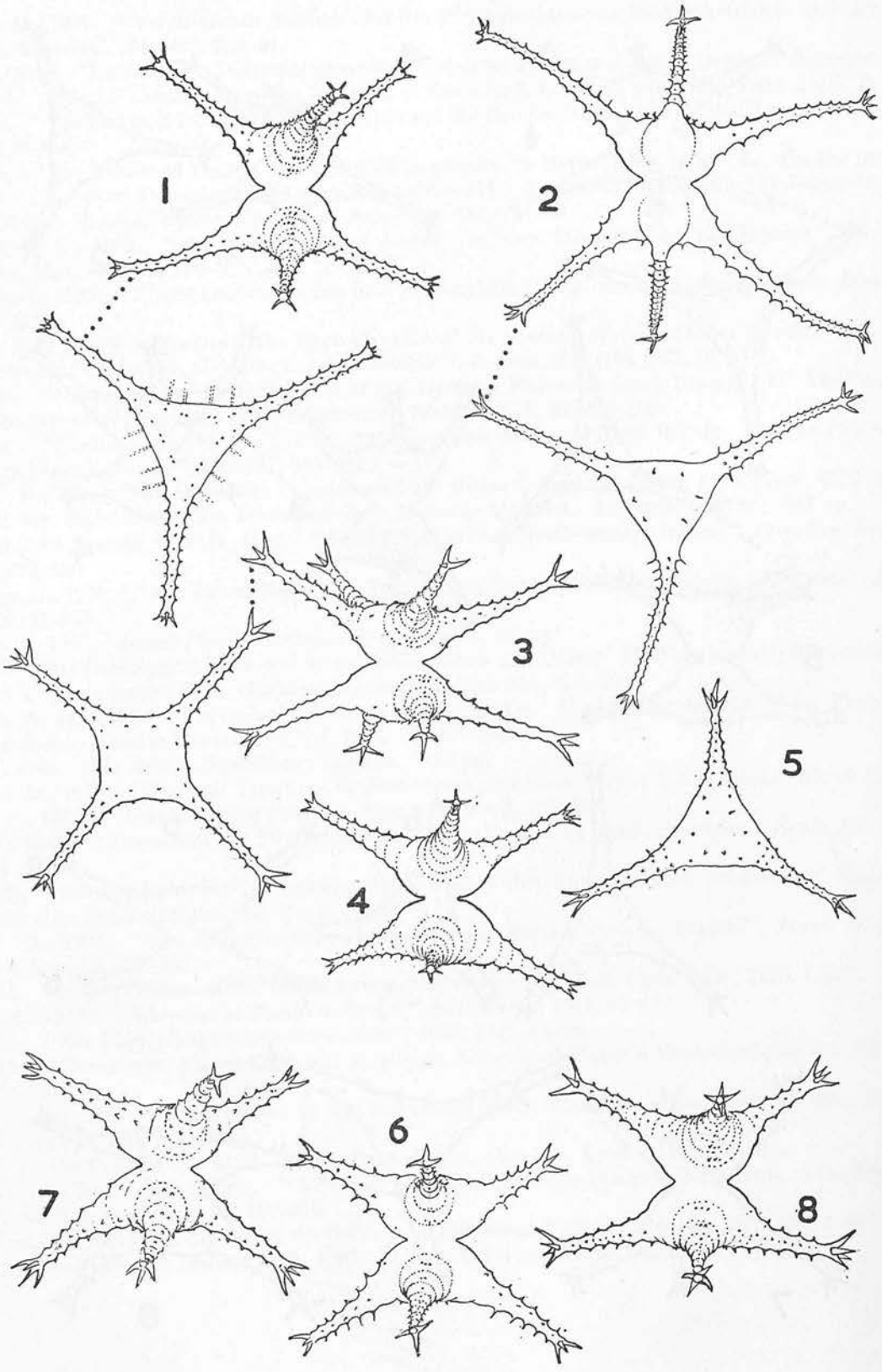

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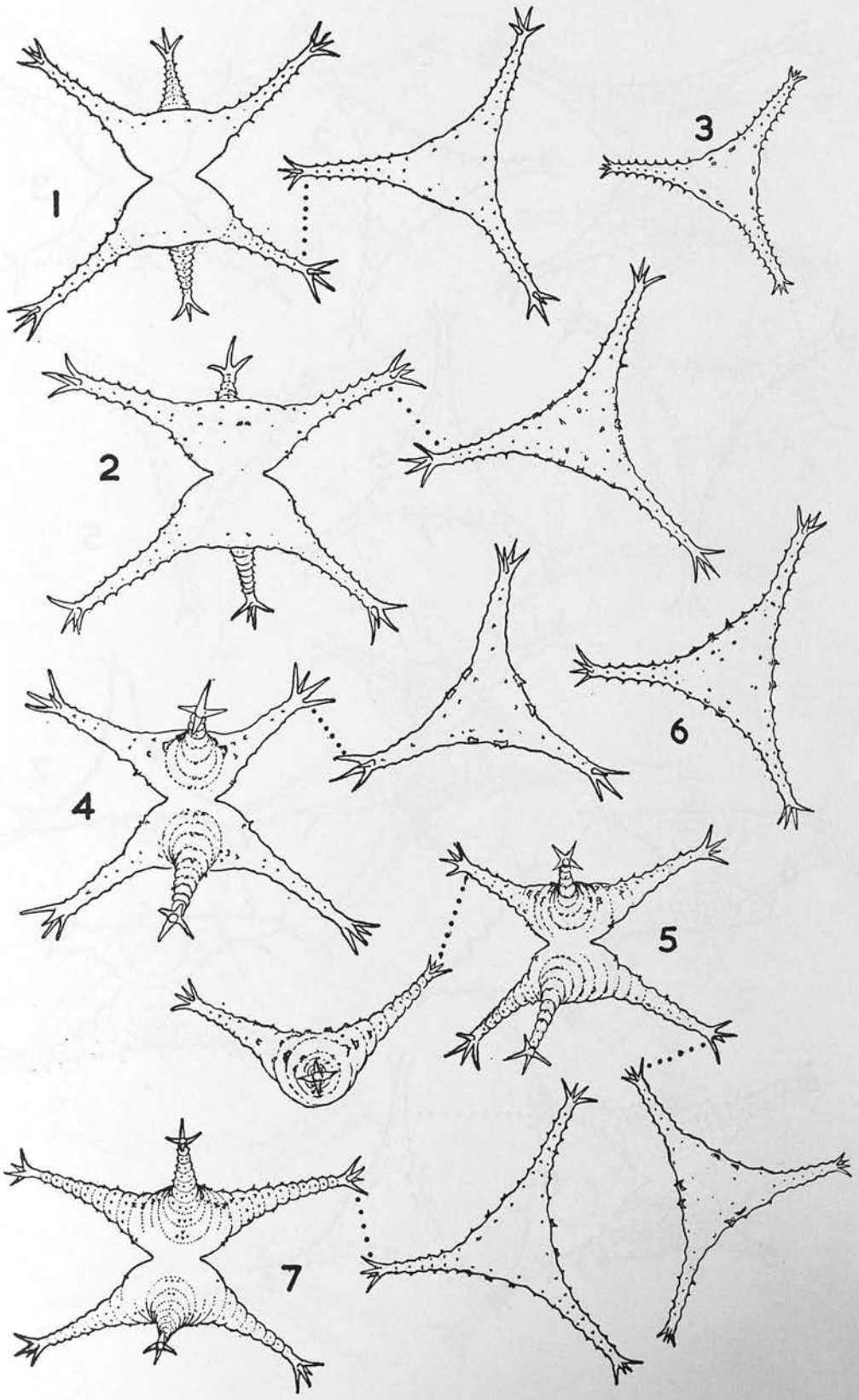

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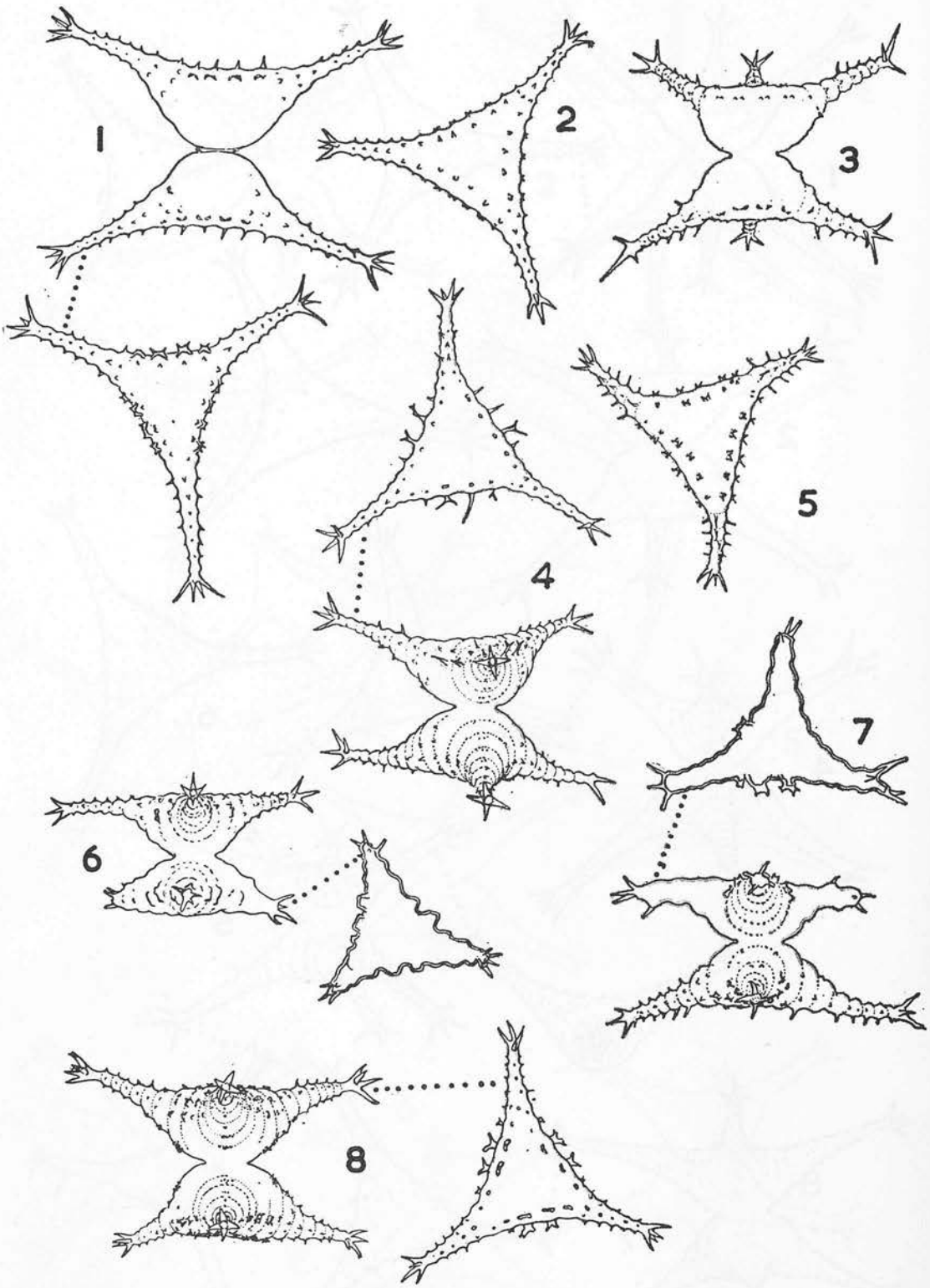

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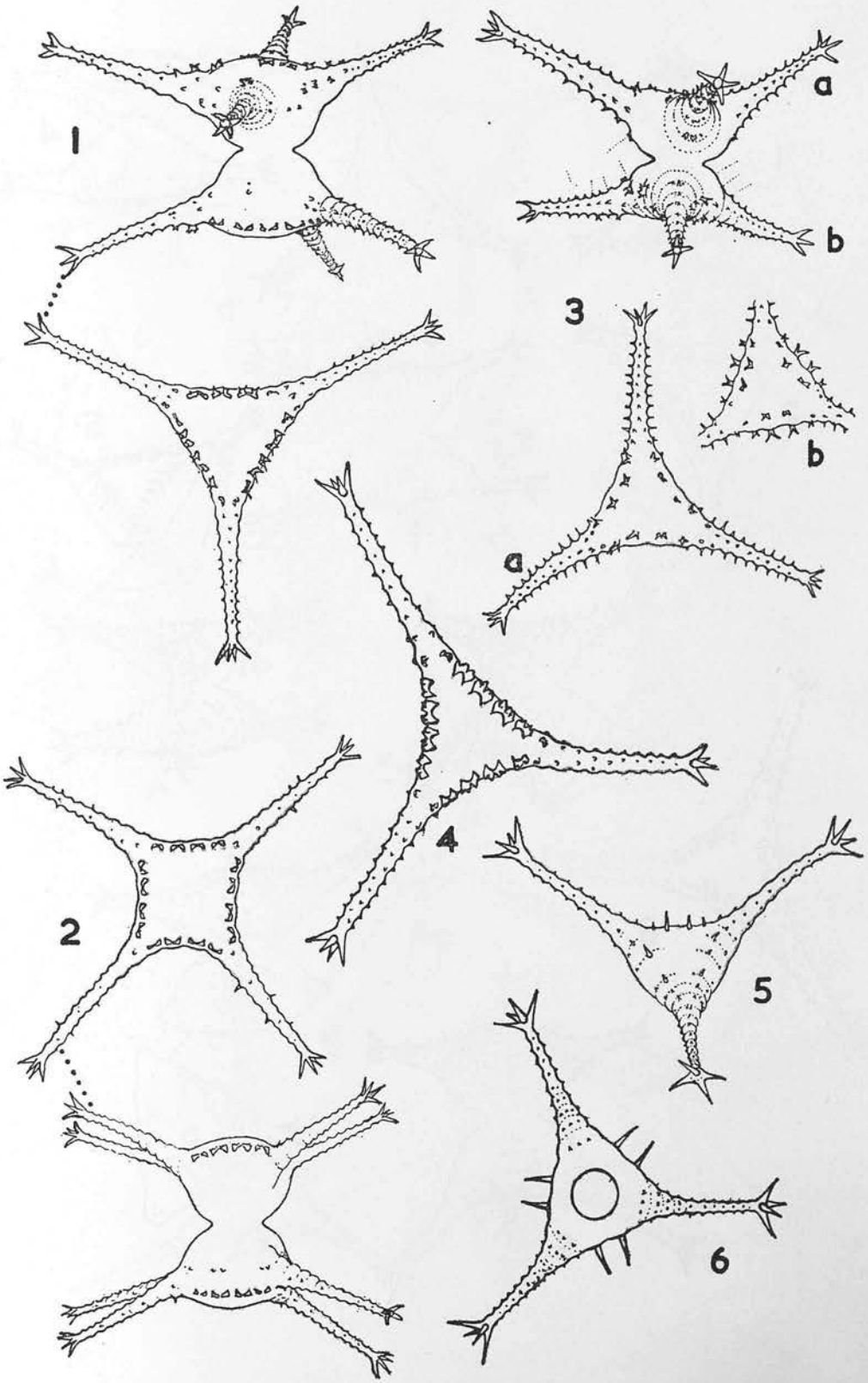

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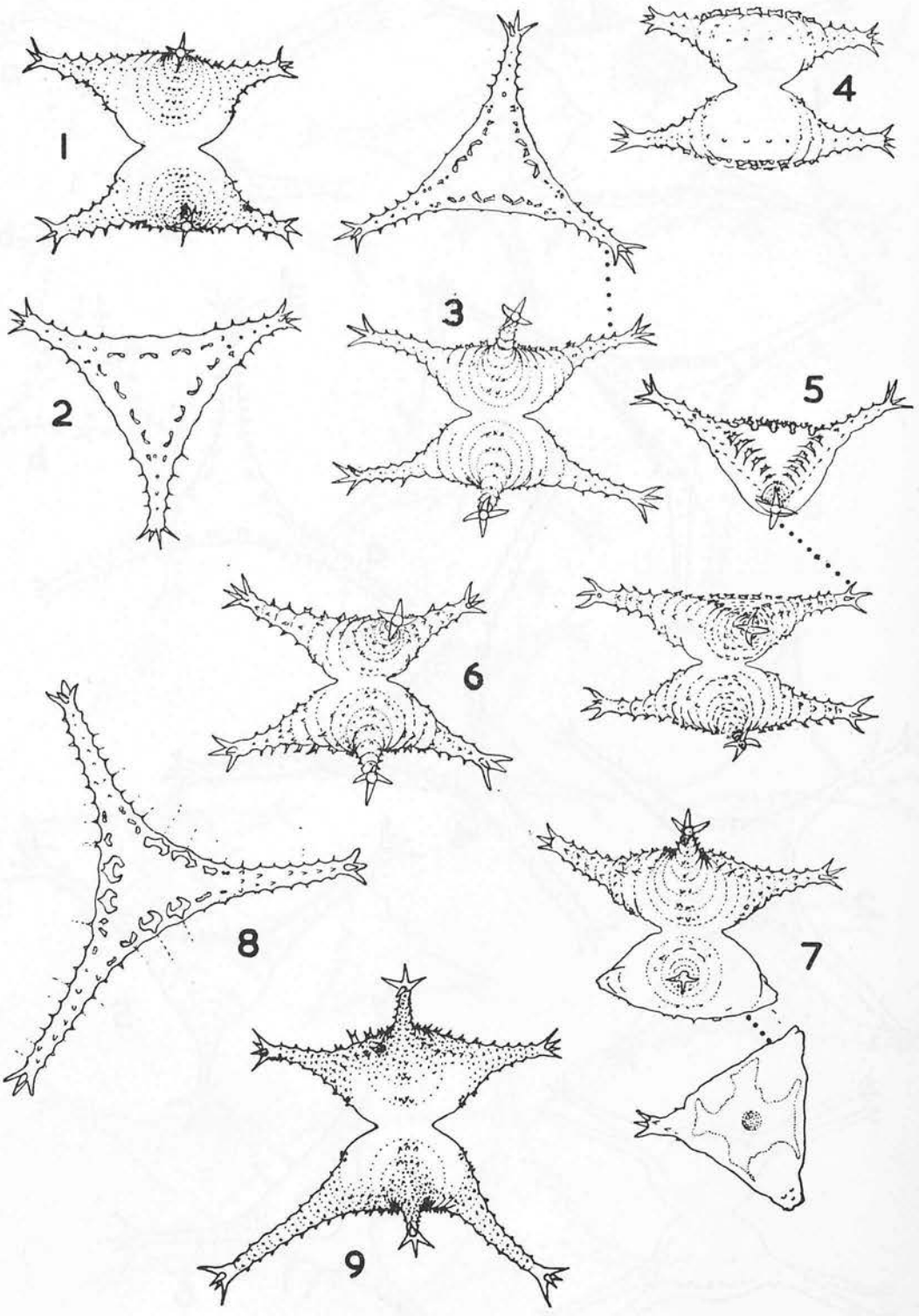

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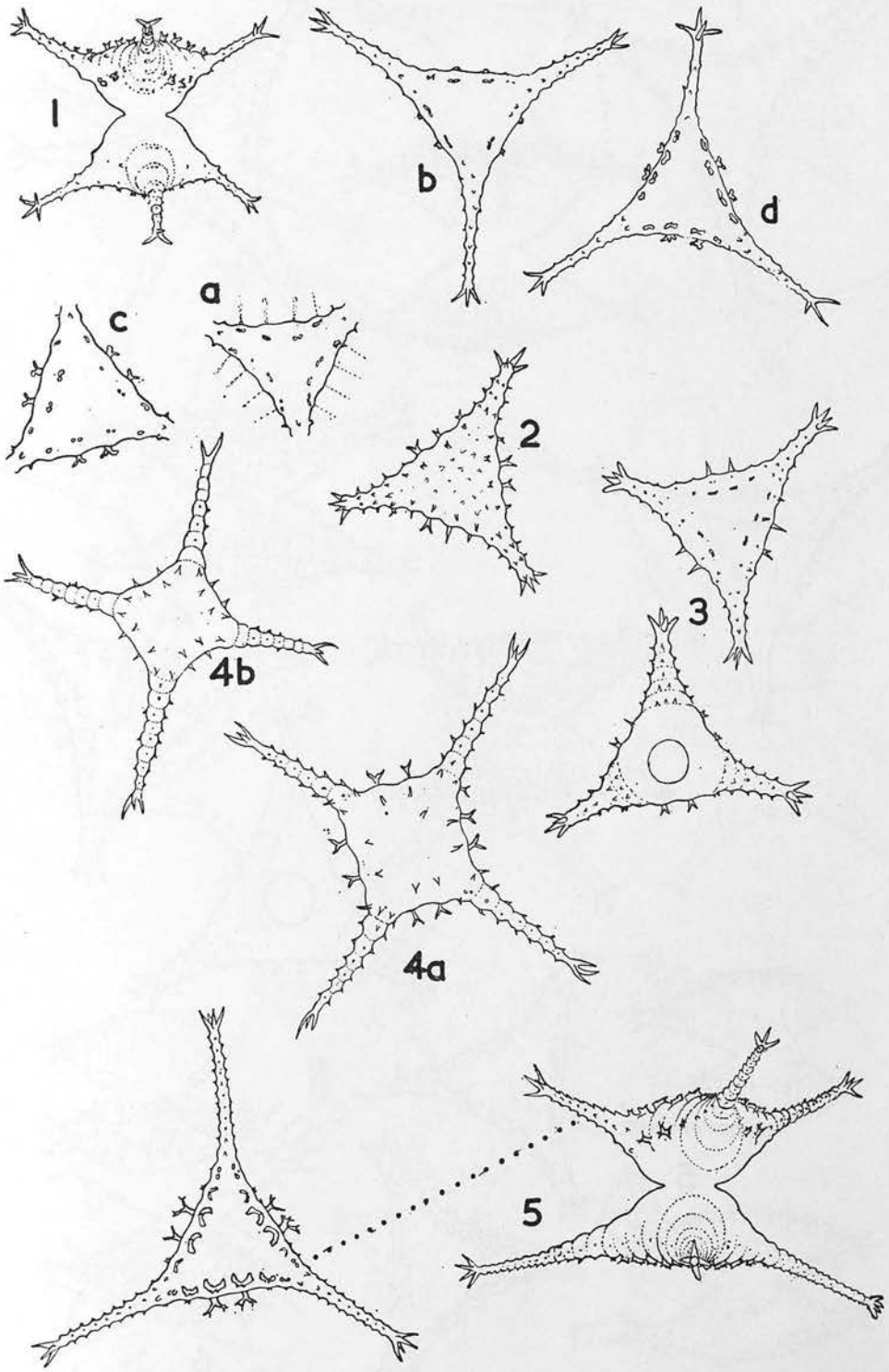

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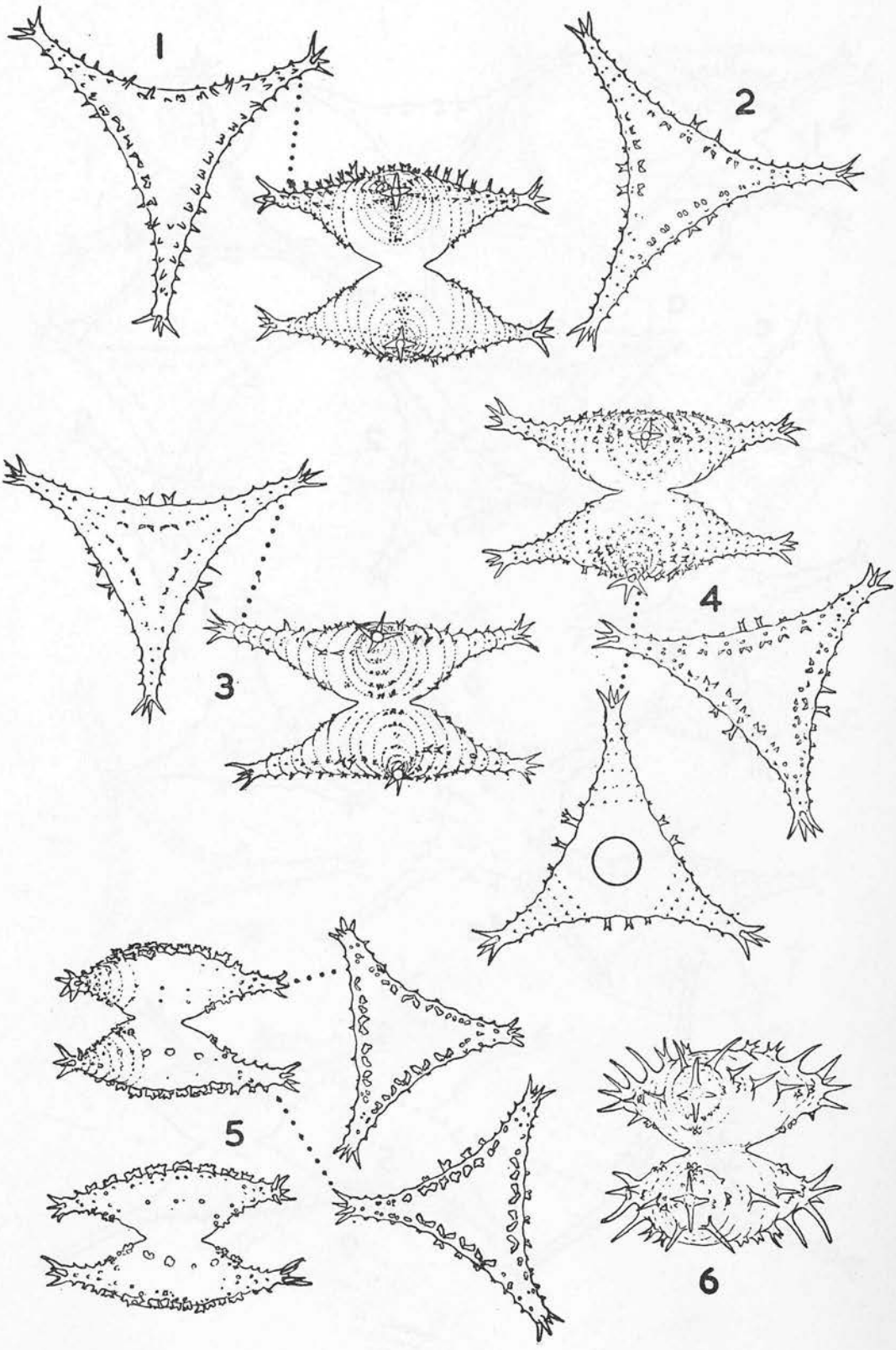

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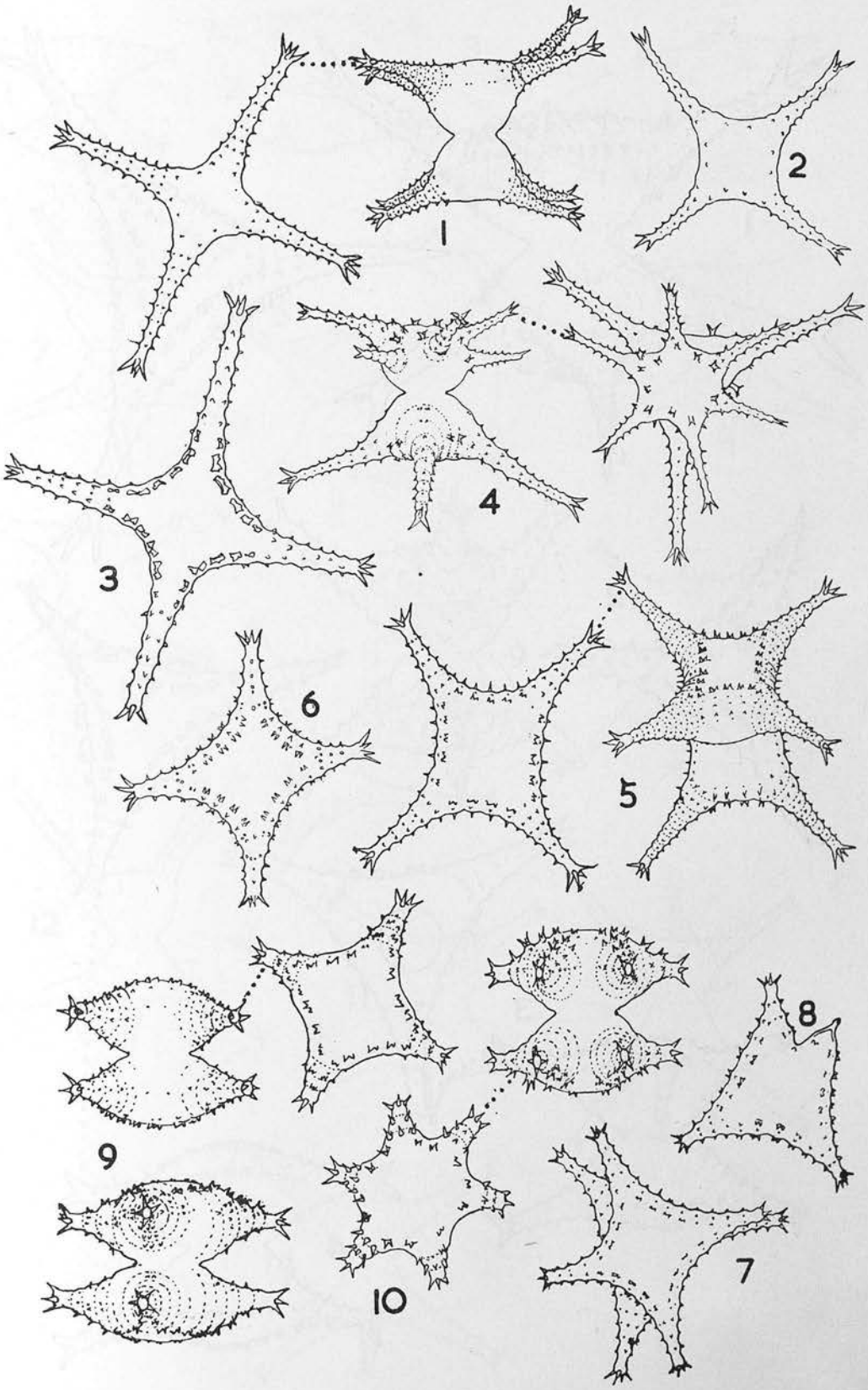

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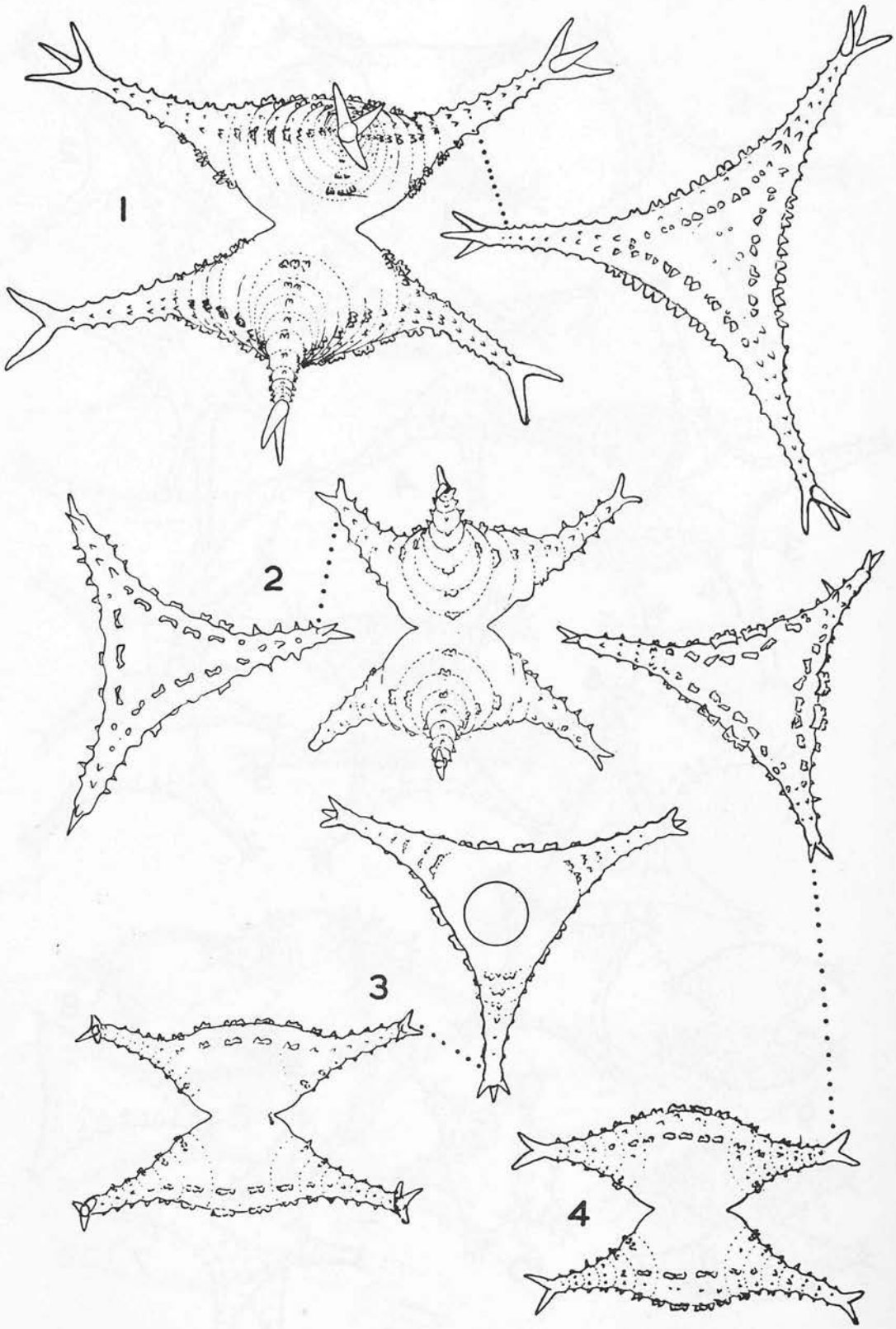

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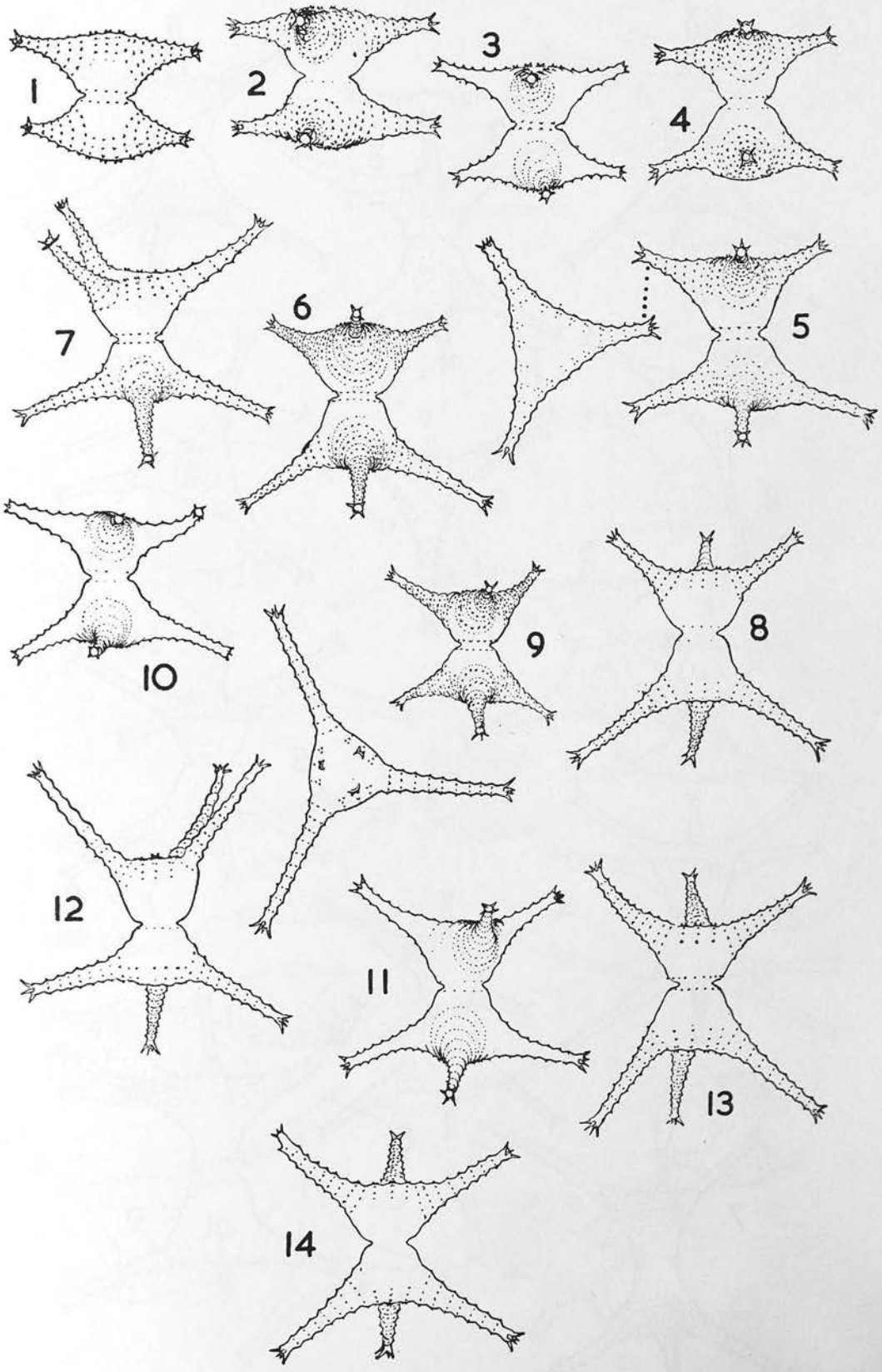

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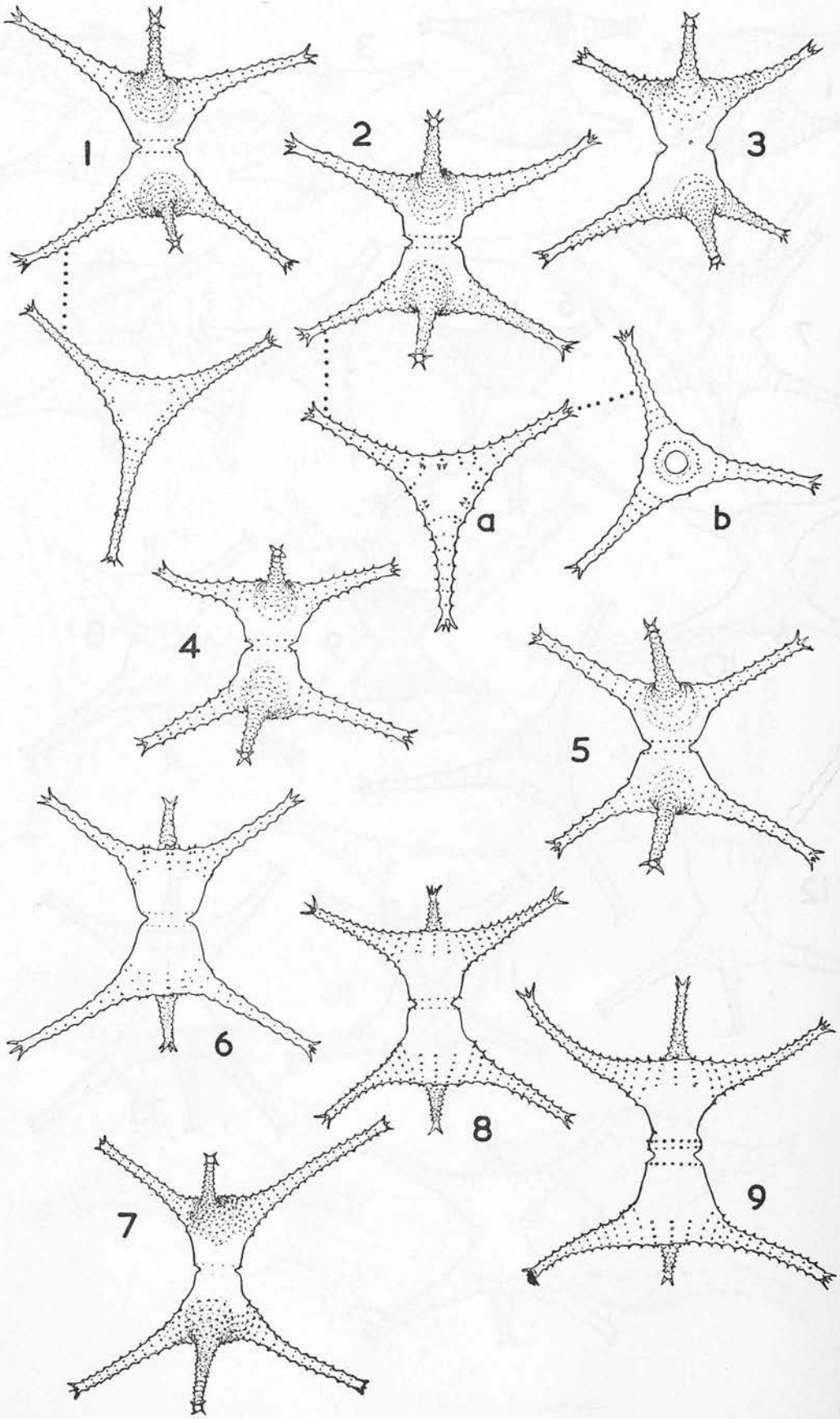

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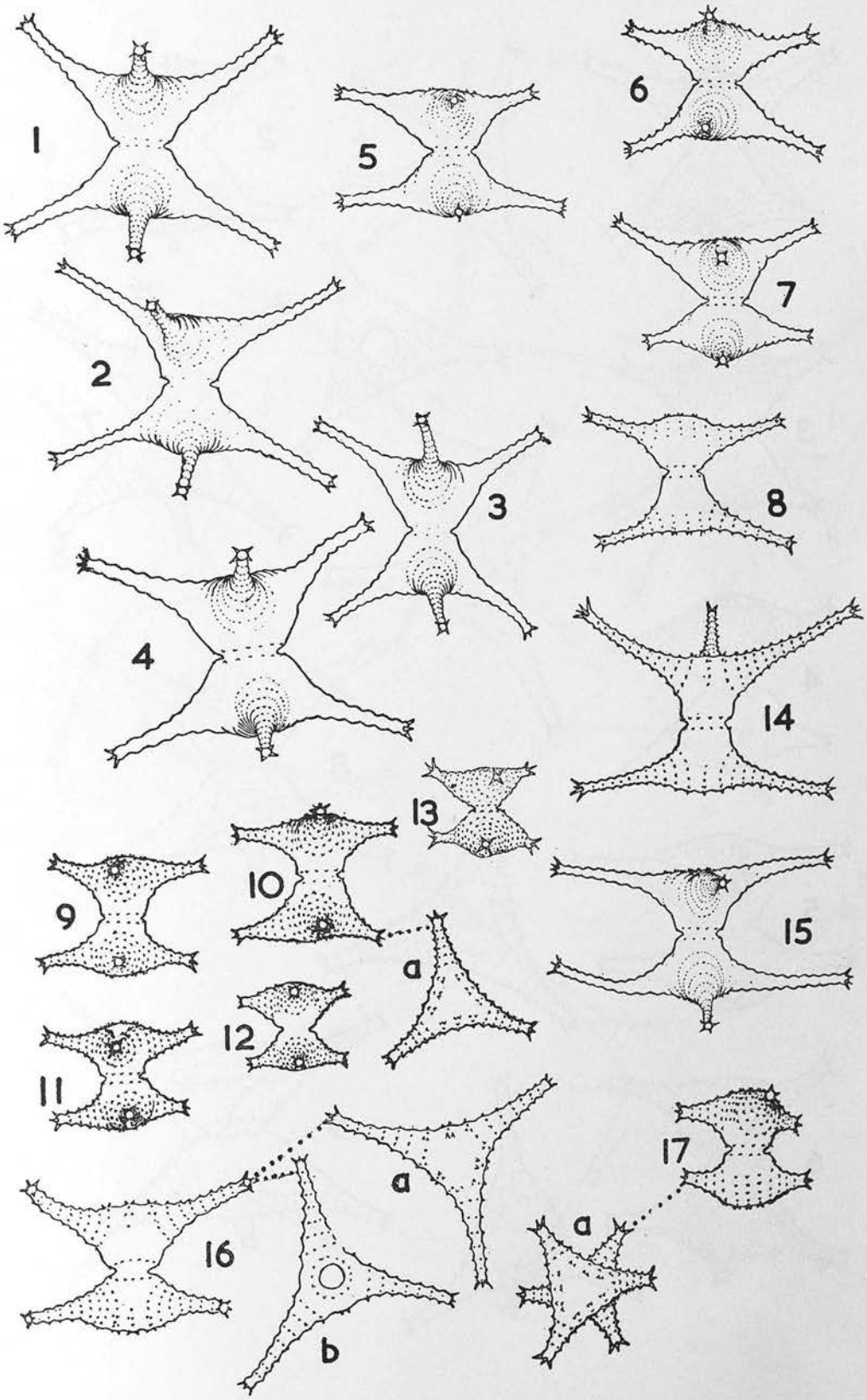

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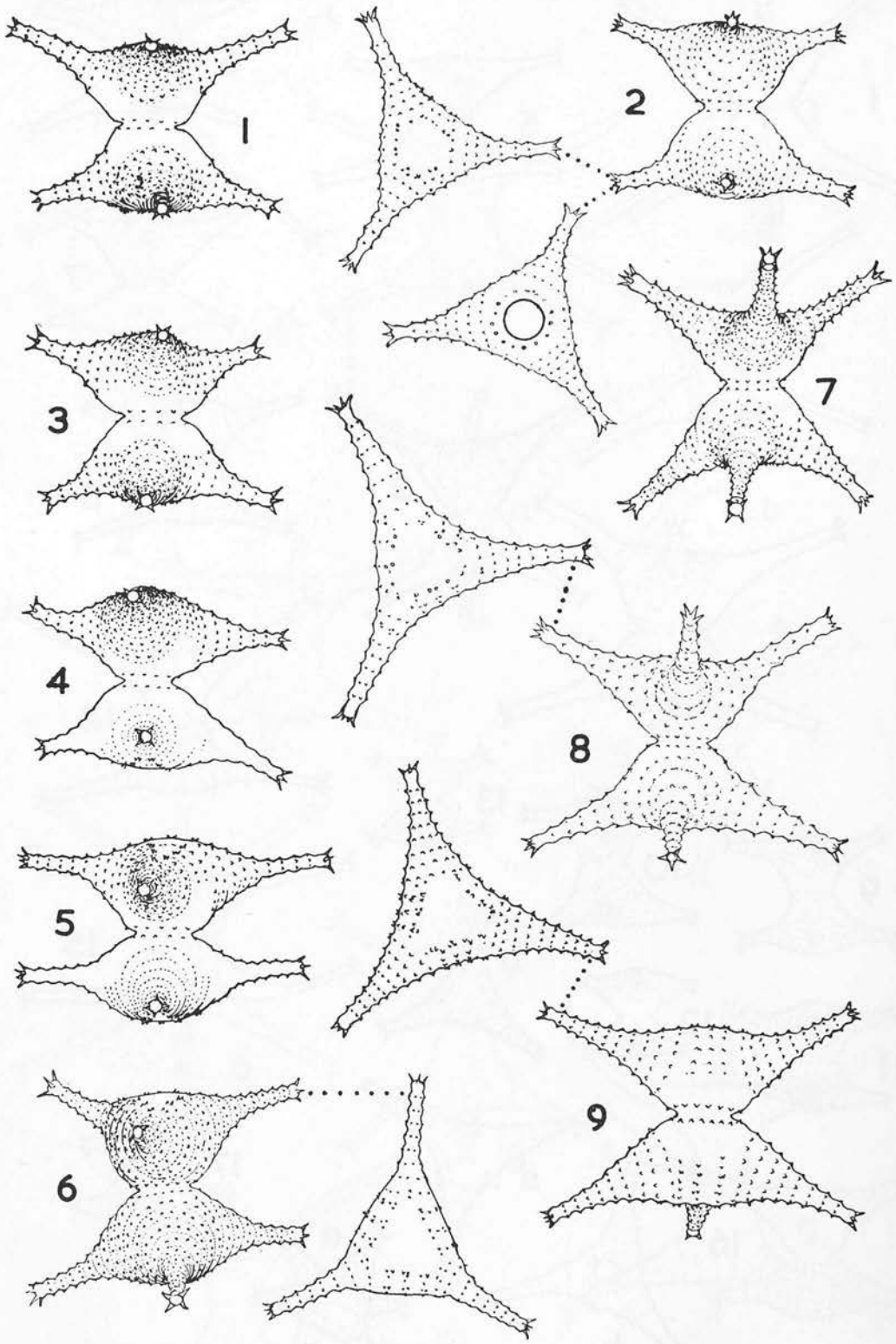
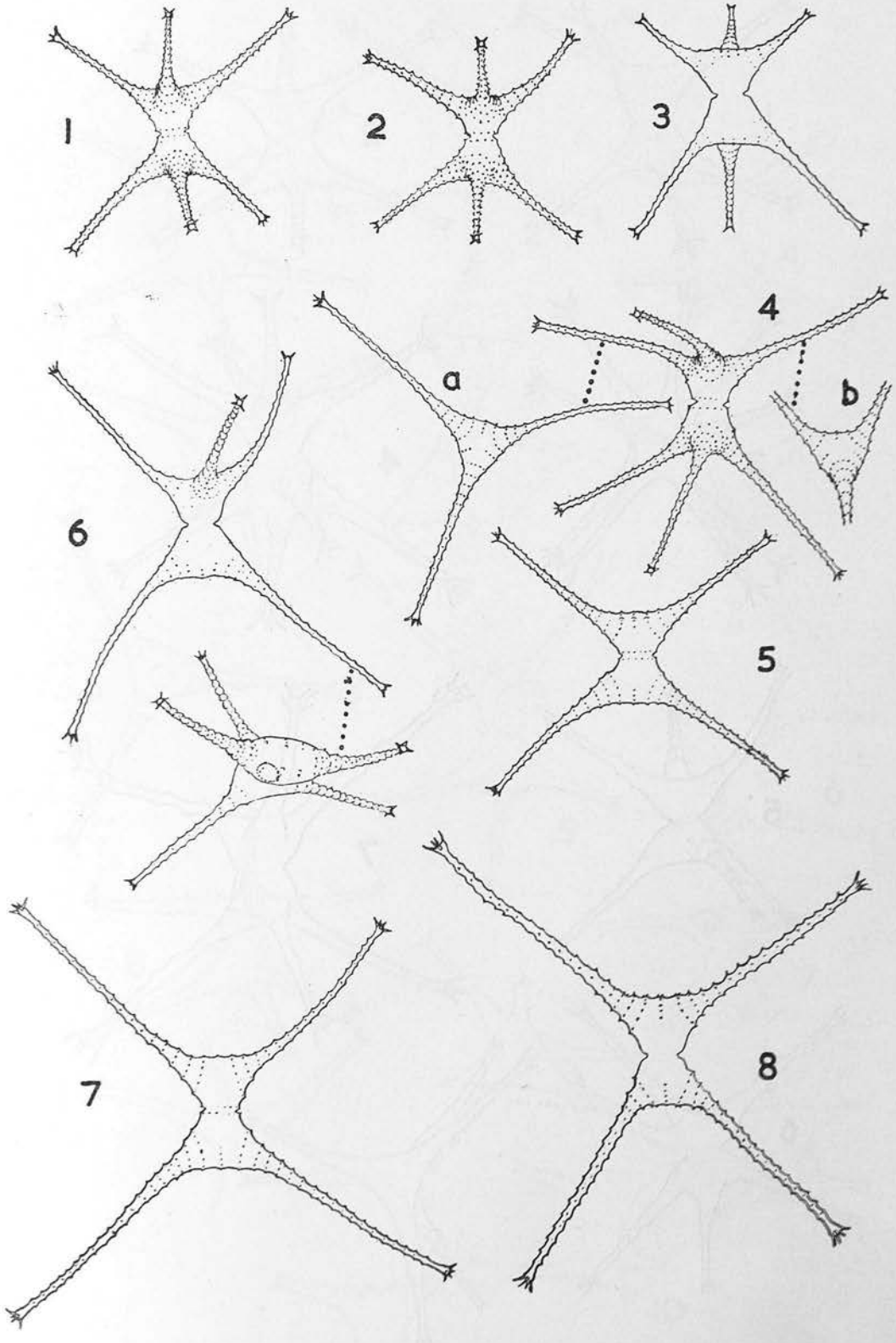
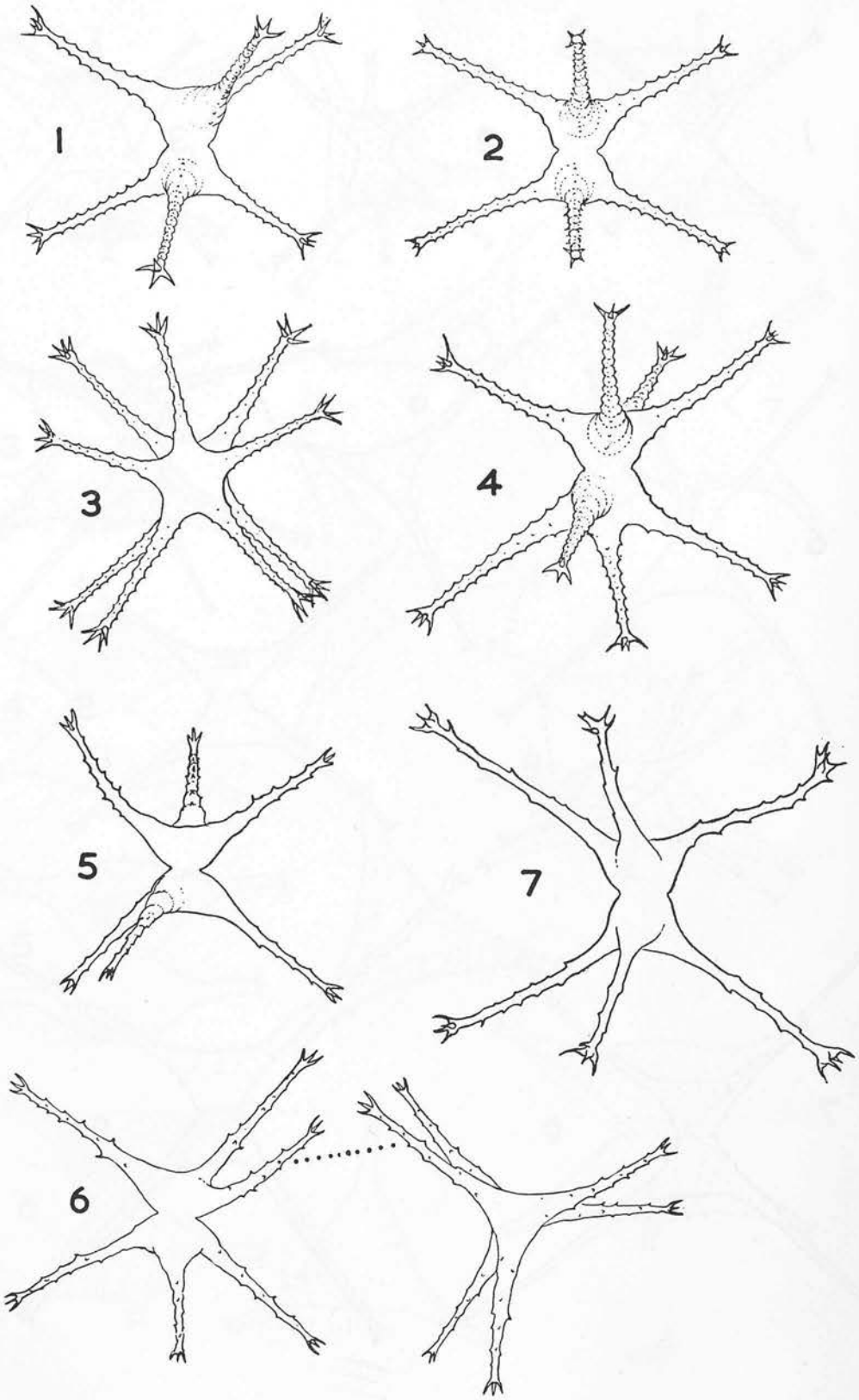


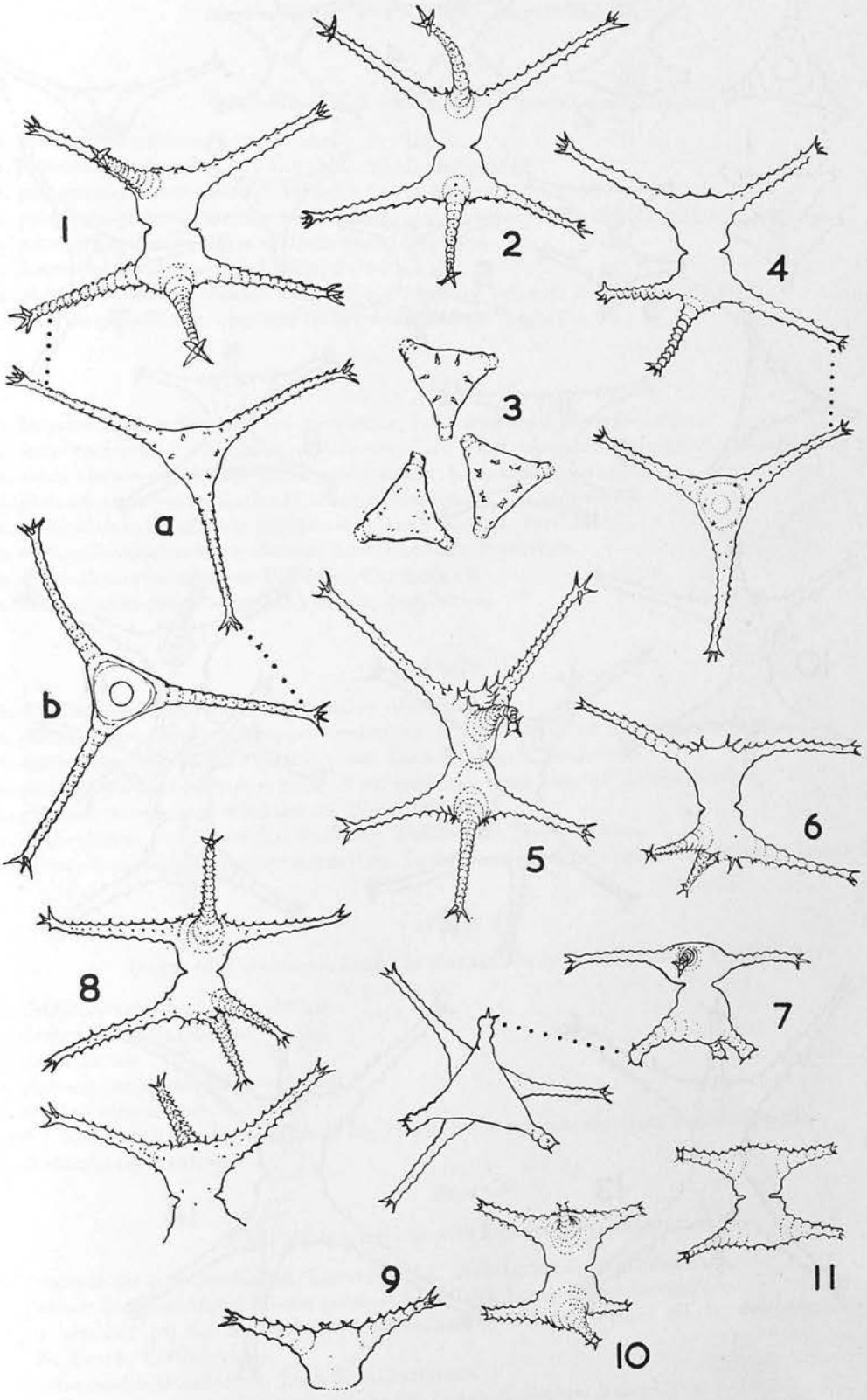
A. J. BROOK, "*Staurastrum paradoxum* Meyen and *S. gracile* Ralfs in the British Freshwater Plankton, and a Revision of the *S. anatinum*-group of Radiate Desmids".—PLATE XV.



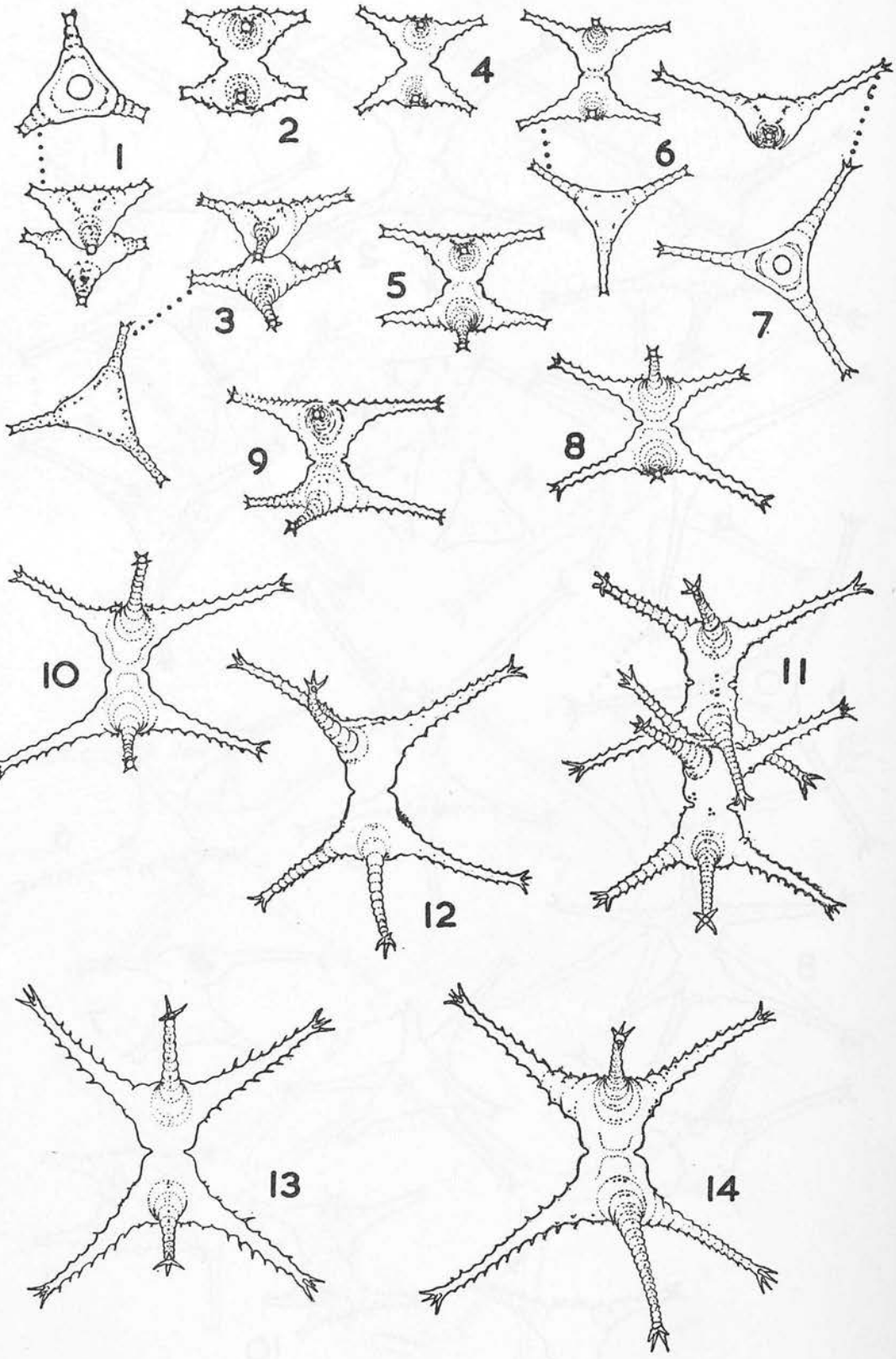
A. J. BROOK, "*Staurastrum paradoxum* Meyen and *S. gracile* Ralfs in the British Freshwater Plankton, and a Revision of the *S. anatinum*-group of Radiate Desmids".—PLATE XVI.



A. J. BROOK, "*Staurastrum paradoxum* Meyen and *S. gracile* Ralfs in the British Freshwater Plankton, and a Revision of the *S. anatinum*-group of Radiate Desmids".—PLATE XVII.



A. J. BROOK. "*Staurastrum paradoxum* Meyen and *S. gracile* Ralfs in the British Freshwater Plankton, and a Revision of the *S. anatinum*-group of Radiate Desmids".—PLATE XVIII.



8. Index to Plates

(All figures drawn to same magnification ×600.)

Plate I

Small forms of *S. anatinum* with *paradoxum* characters.

Fig. 1 fa. *glabrum-paradoxum*, Loch Rannoch, Perthshire.
,, 2 fa. *glabrum-paradoxum*, Loch Loyal (Laoghal), Sutherland.
,, 3 fa. *pelagicum-glabrum-paradoxum*, Loch Loyal, Sutherland.
,, 4 fa. *pelagicum-glabrum-paradoxum* (with aberrant lower semicell), Loch Loyal, Sutherland.
,, 5 fa. *paradoxum*, from culture of Loch Rannoch plants.
,, 6 fa. *hirsutum-paradoxum*, Loch Shin, Sutherland.
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,, 2 fa. *longibrachiatum-denticulatum-paradoxum*, Loch Tarff, Inverness-shire (cf. *S. bullardii* G. M. Smith).
,, 3 fa. *denticulatum-paradoxum* facies *quadriradiata*, Loch Chalium, Caithness.
,, 4 fa. *glabrum-paradoxum*, Loch of Collaster, Shetland.
,, 5 fa. *denticulatum-paradoxum* (apical view), Loch Katrine, Perthshire.
,, 6 fa. *curtum-denticulatum-paradoxum*, Loch Rannoch, Perthshire.
,, 7 fa. *denticulatum-paradoxum*, Ullswater, Cumberland.
,, 8 fa. *denticulatum-paradoxum*, Loch Morar, Argyllshire.

Plate III

Fig. 1 fa. *denticulatum-paradoxum*, Haweswater, Westmorland.
,, 2 fa. *denticulatum-paradoxum* (upper semicell nr. fa. *vestitum*), Loch Lomond, Dunbartonshire.
,, 3 fa. *denticulatum-paradoxum* (apical view), Loch Eagheach, Perthshire.
,, 4 fa. *glabrum-paradoxum* (upper semicell nr. *vestitum*), Loch Lomond, Dunbartonshire.
,, 5 fa. *glabrum-paradoxum*, Windermere, Westmorland.
,, 6 fa. *denticulatum-paradoxum* (nr. *vestitum*), Windermere, Westmorland.
,, 7 fa. *hirsutum-paradoxum* (upper semicell nr. fa. *vestitum*, lower semicell nr. fa. *glabrum*), Lough Gorid, Ireland.

Plate IV

Forms of *S. anatinum* from the plankton of Loch Kinardochy, Perthshire.

Fig. 1 fa. *denticulatum-paradoxum-vestitum*.
,, 2 fa. *denticulatum-paradoxum*.
,, 3 fa. *denticulatum*.
,, 4 fa. *glabrum* (nr.) *-paradoxum-vestitum*.
,, 5 fa. *denticulatum-tortum*.
Figs. 6 and 7 forms with aberrant semicells but in which the *vestitum* character is still apparent.
Fig. 8 fa. *denticulatum-vestitum*.

Plate V

Forms of *S. anatinum* with *longibrachiatum* character.

Fig. 1 fa. *denticulatum-longibrachiatum*, Janus 3 and 4, Loch Lomond, Dunbartonshire.
,, 2 fa. *glabrum-longibrachiatum*, facies *quadriradiata*, Loch Lomond, Dunbartonshire.
,, 3 upper semicell (*a*) fa. *denticulatum-longibrachiatum*. Lower semicell (*b*) fa. *denticulatum-vestitum*, Loch Eagheach, Perthshire.
,, 4 fa. *anatinum-longibrachiatum*, Loch Ness, Inverness.
,, 5 fa. *longibrachiatum-paradoxum* (oblique view), Lough Kylemore, Ireland.
,, 6 fa. *longibrachiatum-paradoxum-vestitum* (transverse view), from same population as fig. 5.

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Fig. 1 fa. *denticulatum-curtum*, Loch Aithness, Shetland.
,, 2 fa. *denticulatum-curtum* (apical view), Derwentwater, Cumberland.
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,, 4 fa. *denticulatum* (cf. *S. eurycerum*, Skuja), Loch Scye, Caithness.
,, 5 fa. *denticulatum*, Loch Shurrery, Caithness.
,, 6 fa. *denticulatum*, Loch Scye, Caithness (*cf.* fig. 4).
,, 7 fa. *hirsutum* (lower semicell aberrant), Crummock Water, Cumberland.
,, 8 fa. *typica* (apical view), Loch Eagheach, Perthshire.
,, 9 fa. *hirsutum*, Lough Beltra, Ireland.

Plate VII

Forms of *S. anatinum* with *vestitum* characters.

Fig. 1 upper semicell fa. *pelagicum-glabrum-vestitum* (see also 1*a* and 1*d*). Lower semicell fa. *pelagicum-glabrum* (see also 1*b* and 1*c*).
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,, 3 fa. *curtum-denticulatum-vestitum* (apical and transverse views), Loch Scye, Caithness.
,, 4*a* fa. *denticulatum-paradoxum-vestitum* facies *quadriradiata*.
,, 4*b* from same population but *vestitum* character less pronounced (see also Pl. II, fig. 3, and Pl. IX, fig. 4).
,, 5 upper semicell and apical view fa. *longibrachiatum-denticulatum-vestitum*. Lower semicell fa. *longibrachiatum-glabrum*, Loch Lomond, Dunbartonshire (see Pl. V, figs. 1 and 2).

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,, 3 fa. *hirsutum-vestitum*, Buttermere, Cumberland.
,, 4 fa. *hirsutum-vestitum*, Loch Mhor, Inverness-shire.
,, 5 fa. *curtum-hirsutum-vestitum* (nr. var. *aculeatum*), Loch Arklet, Perthshire.
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Plate IX

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,, 2 fa. *denticulatum-paradoxum* facies *quadriradiatum*, Loch Chalium, Caithness (*cf.* Pl. II, fig. 3).
,, 3 fa. *anatinum* facies *quadriradiata*, Lake of Menteith, Perthshire.
,, 4 fa. *denticulatum-vestitum*, Janus 3 and 6, Loch Eagheach, Perthshire.
,, 5 fa. *hirsutum* facies *quadriradiata*, Lough Beltra, Ireland.
,, 6 fa. *curtum-hirsutum* facies *quadriradiata*, Loch Mhor, Inverness-shire.
,, 7 fa. *hirsutum*, Janus 3 and 4, Loch Mhor, Inverness-shire.
,, 8 fa. *hirsutum*, aberrant facies *quadriradiata*, Loch Mhor, Inverness-shire.
,, 9 fa. *curtum-hirsutum* facies *quadriradiata*, Loch Mhor, Inverness-shire.
,, 10 fa. *curtum-hirsutum* facies *sexcostatum* (=*S. sexcostatum* Breb), Loch Mhor, Inverness-shire.
N.B.—Figs. 5–10 make up a series showing reduction in process length and increasing radiation.

Plate X

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,, 2 *S. anatinum* var. *truncatum*, Loch Lomond, Dunbartonshire.
,, 3 *S. anatinum* var. *truncatum*, Ridge Loch, Sutherland.
,, 4 *S. anatinum* var. *truncatum*, Lough Ardderry, Ireland.

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Fig. 1 *S. gracile*, Loch Calavie, Ross and Cromarty.
,, 2 *S. gracile*, Littleton Reservoir, Renfrewshire.
,, 3 *S. gracile* forma, Ridge Loch, Sutherland.
,, 4 *S. gracile* forma, Balgray Reservoir, Renfrewshire.
,, 5 *S. cingulum*, a robust form, upper semicell nr. *S. gracile*, Loch Leven, Kinross-shire.
,, 6 *S. cingulum*, a dichotypical form, timid upper semicell nr. *S. gracile*, Loweswater, Cumberland.
,, 7 *S. cingulum*, *dichotypical* form, body of upper semicell nr. *S. gracile*, Loch Shin, Sutherland.
,, 8 *S. cingulum*, dichotypical form, Windermere, Westmorland.
,, 9 *S. cingulum*, small form nr. *S. gracile*, Eye Brook Reservoir, Northamptonshire.
,, 10 *S. cingulum*, Loch Fiart, Lismore.
,, 11 *S. cingulum*, Loch Balnagowan, Lismore.
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PLATE XII

Fig. 1 *S. cingulum*, Loch Lomond, Dunbartonshire.
,, 2 *S. cingulum*, Loweswater, Cumberland.
,, 3 *S. cingulum*, Crummock Water, Cumberland.
,, 4 *S. cingulum*: (*a*) apical, (*b*) transverse view, Ullswater.
,, 5 *S. cingulum*, Ullswater, Westmorland (*cf.* lower semicell with lower semicell of Pl. XI, fig. 5).
,, 6 *S. cingulum*, with prominent apical ornamentation (*cf.* Pl. XI, fig. 12) and elongated body, Windermere, Westmorland.
,, 7 *S. cingulum*, elongated form, Loch Morar Inverness-shire.
,, 8 *S. cingulum*, elongated form, Loch Shin, Sutherland.
,, 9 *S. cingulum* fa. *annulatum*, Loch Shin.

PLATE XIII

Fig. 1 *S. cingulum*, robust form.
,, 2 *S. cingulum*, nr. typical form.
,, 3 *S. cingulum*, short-armed form.
,, 4 *S. cingulum*, nr. var. *obesum*.
Figs. 1–4 are all from the same sample, from Loch Garth, Inverness-shire.
,, 5 *S. cingulum* nr. *S. gracile*, Waukmill Reservoir, Renfrewshire.
,, 6 *S. cingulum* nr. *S. gracile*, Loch Hosta, N. Uist.
,, 7 *S. cingulum*, dichotypical form, lower semicell, especially nr. *S. gracile*, Loch Hosta, N. Uist.
,, 8 *S. cingulum*, small form, Loch Kilcherean, Lismore.
Figs. 9–13 *S. boreale*, Lough Boffin, Ireland.
Fig. 14 *S. boreale* var. *planctonicum*, Loch Calavie, Ross and Cromarty.
,, 15 *S. boreale* var. *planctonicum*, Loch Ness, Inverness-shire.
,, 16 *S. boreale* var. *planctonicum*, Loch Tingwall, Shetland.
,, 17 *S. gracile*, Lough Boffin, Ireland.

PLATE XIV

Fig. 1 *S. cingulum*, Loch Garth (Pl. XIII, figs. 1–4).
,, 2 *S. cingulum* var. *affine*, Loch Scye, Caithness.
Figs. 3–5 *S. cingulum* var. *affine*, Loch Aithness, Shetland.
Fig. 6 *S. cingulum* var. *affine*, Loch of Girlista, Shetland.
,, 7 *S. cingulum* var. *obesum*, Derwentwater, Cumberland.
,, 8 *S. cingulum* var. *obesum*, Loweswater, Cumberland.
,, 9 *S. cingulum* var. *obesum*, Loch Kinardochy, Perthshire.

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Figs. 1 and 2 *S. chætoceras*, small forms, Eye Brook Reservoir, Northamptonshire.
Fig. 3 *S. chætoceras*, small form, Swithland Reservoir, Leicestershire.
,, 4 *S. chætoceras*, Lough Erne, Ireland.

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,, 4*b* oblique view of apex.
Figs. 5 and 7 *S. chœtoceras* facies *biradiata*, Lough Erne, Ireland.
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Plate XVI

Fig. 1 *S. longipes*, Lough Ballynahinch, Ireland.
,, 2 *S. longipes* var. *contractum*, Loch Olavat, Benbecula.
,, 3 *S. longipes*, Janus 4+5, Loch Shurrery, Caithness.
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Plate XVII

Figs. 1 and 2 *S. pingue*, Loch Kinardochy, Perthshire. (*a*) Apical view, (*b*) transverse view.
Fig. 3 *S. pingue*, Loch Kinardochy, apical views of several individuals showing variation of apical ornamentation.
,, 4 *S. pingue*, Loch Earn, Perthshire.
,, 5 *S. pingue*, Kylemore Lough, Ireland.
,, 6 *S. pingue*, Loch of Girlista, Shetland.
,, 7 *S. pingue*, aberrant form, Loch of Girlista.
,, 8 *S. pingue*, Loch Shin, Sutherland.
,, 9 *S. pingue*, Bassenthwaite, short-armed form.
,, 10 *S. pingue*, Loch Grasswater, Shetland.
,, 11 *S. pingue*, Loch Spiggie, Shetland.
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Plate XVIII

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Fig. 4 *S. crenulatum*, Cameron Reservoir, Fifeshire.
,, 5 *S. pingue*, small form, Saddington Reservoir.
Figs. 6–8 *S. pingue*, small form, Eye Brook Reservoir.
Fig. 9 *S. pingue*, small form, Loch Hosta, N. Uist.
,, 10 *S. pingue*, Loch Leven, Kinross.
,, 11 *S. pingue*, Bassenthwaite, prominent decoration of semicells as in *S. leutkemuelleri*.
,, 12 *S. pingue*, Loch of Lindores, Fifeshire.
,, 13 *S. pingue*, Loch Leven, Kinross-shire.
,, 14 *S. pingue*, Balgavies Loch, Forfarshire.
Figs. 12–14 are of forms approaching Teiling's *S. planctonicum*.

TRANSACTIONS

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VOLUME LXIII, PART III, 1958–59

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26. Staurastrum paradoxum *Meyen and* S. gracile *Ralfs in the British Freshwater Plankton, and a Revision of the* S. anatinum*-group of Radiate Desmids.* By A. J. BROOK, Ph.D., F.L.S., Freshwater Fisheries Laboratory, Pitlochry, Scotland. *Communicated by* Professor J. R. MATTHEWS, C.B.E. (With Eighteen Plates and Four Text-figures.) Price: 17*s.* 6*d.* (*Issued November* 9, 1959.)

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De Brébisson's Determinations of Staurastrum paradoxum Meyen and S. gracile Ralfs

by A. J. Brook, Edinburgh.

With plates 28 (1) — 29 (2).

The names S. *paradoxum* and S. *gracile* appear in the literature under figures representing very many species of *Staurastrum*. In the case of the former species, for which unfortunately no type material exists, these illustrations have been critically examined and separated into ten well defined and adequately described taxa (Brook 1959 b). For S. *gracile*, the type material from the Jenner Herbarium in the British Museum has been re-examined and the limits of the species redefined (Brook 1959a). Through the courtesy of the Keeper of the Herbarium of the University and Town of Caen, it has been possible to examine material from the algal herbarium of Chauvin which was referred by De Brébisson to these two species.

The packet named S. *gracile* is stated by the Keeper of the Herbarium, M. Le Testu, to be in De Brébisson's own hand. These desmids clearly belong to the *gracile*-group of the genus (Brook 1959a), having the typical apical ornamentation of 3 granula bigemina along each margin (Pl. 1, figs. 7—9). However, on the basis of size, semicell shape, and the fact that the series of granules, wich extend down onto the body of the semicell from the outer 2 of the 3 apical granula bigemina, encircle the processes (cf. Brook, 1959a, p. 600 and Pl. XIII, figs. 9-16), this „*gracile*" material must in fact be referred to S. *boreale* W. & G. S. West.

The material which De Brébisson has determined as being of S. *paradoxum* is however, more or less identical the type material of S. *gracile* from the British Museum (Pl. 1, figs. 1—4) (cf. Brook 1959a Text Fig. 3)! Occasional semicells of S. *boreale* are also present amongst this material along with many other desmid species.

Another packet marked

Staurastrum paradoxum var. incurvum Bréb.

——————— *dejectum* Brébiss.

Falaise.

has been kindly forwarded for examination along with the other material. The name *S. paradoxum* var. *incurvum* immediately poses a problem, since there is no record of this variety in De Brébisson's papers, nor in Ralfs (1848), nor in Nordstedt's *Index Desmidiacearum*. However, there would seem to be little doubt that the most abundant *Staurastrum* on this small slide, with (in side view) its markedly incurved processes and convex apex (Pl. 2, figs. 1—5) is synonomous with Brébisson's *S. brachycerum*, which he has recorded as being rare in Falaise (Brébisson 1856, Pl. 1, fig. 24). There appears to be only one adequate illustration of this apparently rare species, in the literature, (West and Carter 1923, Pl. 142, figs. 21—22), but it corresponds well in essential features with this De Brébisson material, which unfortunately is not in a good state of preservation. All the complete specimens lying in side view are bent or distorted in one way or another (Pl. 2, figs. 2 and 5), but they nevertheless show the characteristic incurved processes and convex apex of this species. A number of well preserved semicells are however present in apical and basal view (Pl. 2, figs. 1, 3 and 4). The former show the apical ornament to consist of 3 small intramarginal spines (occasionally granulae bigeminae), one in the centre of each margin, from which a short series af granules runs down onto the body of the semicell. The basal view of the semicell shows a distinctive isthmal ornamentation of one, two or three small granules opposite each process (Pl. 2, fig. 3).

A desmid which must be referred to *S. brachycerum* has been found in the tychoplankton of Lough Bofin, Ireland. It has been recorded as *S. inflexum* Bréb. (Brook 1958, fig. 60, Round & Brook, 1959), but a re-examination of this Irish material in the light of the interesting De Brébissn material has shown clearly that this determination was erroneous (Pl. 2, figs. 6—8). It can be seen that the processes of the Lough Bofin form are considerably longer than in De Brébisson's plants and in those from which the West and Carter figures were drawn. However, the other characters, and especially the apical and isthmal ornamentation, unquestionably indicate that this desmid is a form of *S. brachycerum*.

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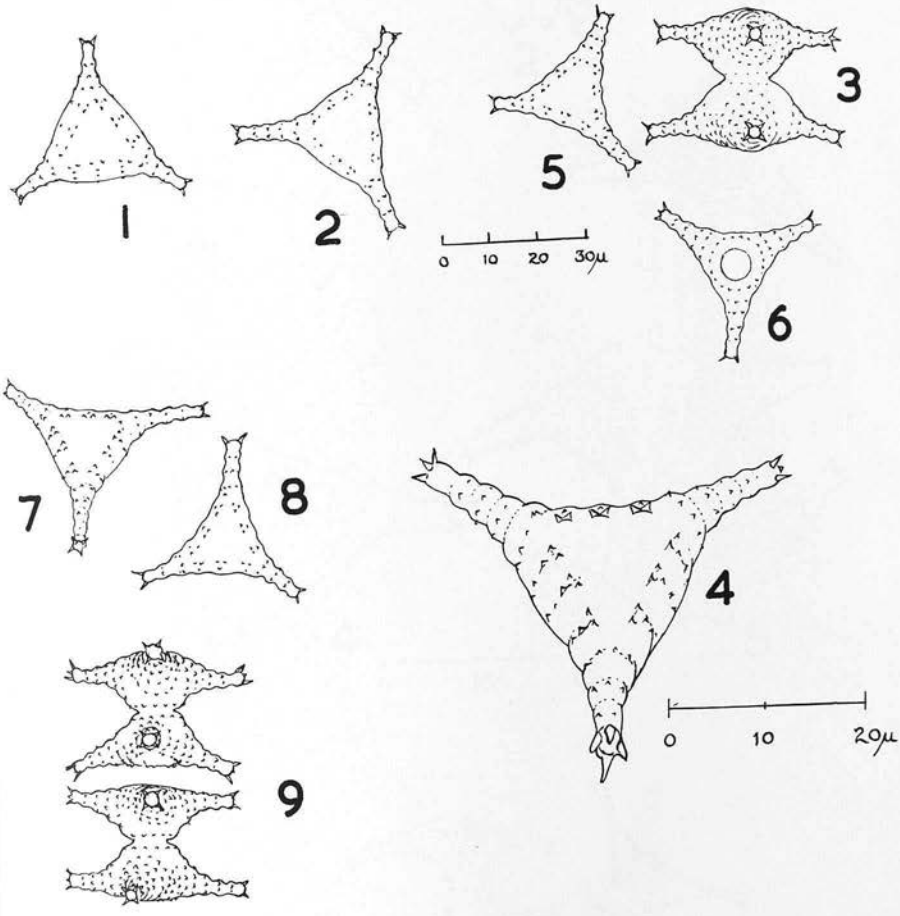
West, G. S. & Carter, N. British Desmidiaceae, Vol. V, London, Ray Society.

EXPLANATION OF THE PLATES:

Plate 28 (1): Figs. 1—4: *Staurastrum gracile* RALFS from material in the algal herbarium of CHAUVIN, determined by DE BRÉBISSON as *S. paradoxum* MEYEN.
Figs. 5—6: *S. boreale* W. & G. S. WEST from the same slide.
Figs. 7—9: *S. boreale* from material labelled in DE BRÉBISSON's own hand as *S. gracile*.

Plate 29 (2): Figs. 1—5: *Staurastrum brachycerum* BRÉB., from material in the CHAUVIN algal herbarium and named by DE BRÉBISSON as *S. paradoxum* var. *incurvum* BRÉB.
Figs. 6—8: A form of *S. brachycerum* from Lough Bofin, Ireland.



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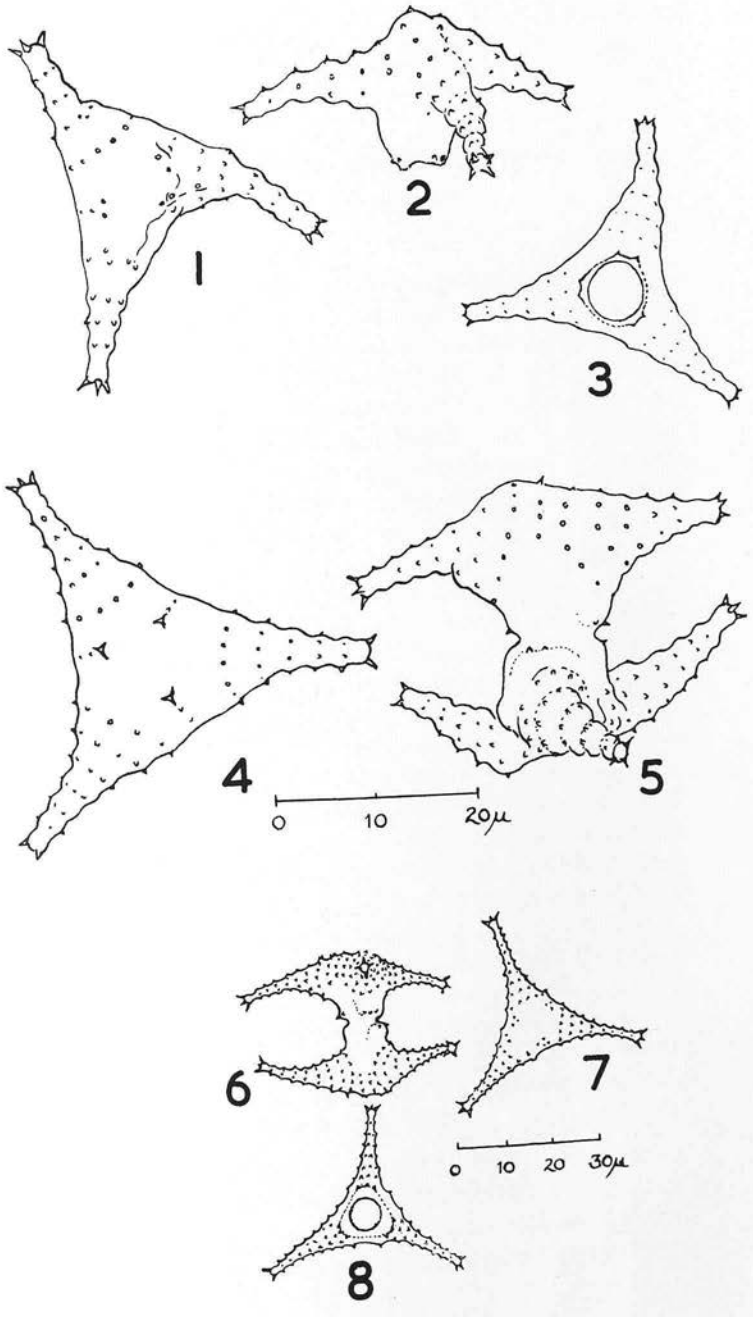

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The Varieties of Staurastrum paradoxum Meyen - nomen dubium

By A. J. Brook, Edinburgh.

With Plates 88 (1) — 91 (4).

Owing to the lack of type material, the inadequacy of the original description and the vast and confusing number of forms subsequently referred to *Staurastrum paradoxum,* it has been proposed to abandon this species (Brook 1959a). Indeed its limits in the course of time have become so vague that almost any *Staurastrum* with well developed processes and little or no semicell ornament would seem to have been referred to it (Brook 1959 b). An inevitable consequence of the existence of such an ill-defined taxon has been the establishment of a large number of varieties, but as with the species, several of these have also become merely convenient names to attach to „difficult" forms. For example, many small Staurastra lacking distinct semicell ornament have been referred to the var. *parvum*, while many forms with long processes have been named, indiscriminately, as var. *longipes*. Since the species itself has no reality, it is clear that none of these varieties can be maintained. Those which have been adequately described and are well defined must either be given specific rank or established as varieties of other good species. This has already been done in certain cases, e. g. Smith 1924, *S. paradoxum* var. *cingulum* (West & West) = *S. cingulum* (West & West) G. M. Smith, *S. paradoxum* var. *chaetoceras* Schröder = *S. chaetoceras* (Schröder) G. M. Smith. However, those varieties which, like the species, are now ill-defined rubbish dumps must become „nomina dubia" and be abandoned.

The purpose of the present paper is to consider each of the varieties of *S. paradoxum* in turn, either in relation to the many illustrations in the literature to which they have been referred, or in some cases by reference to the original material from which they were described, and to attempt to place them in the taxa where it is considered they properly belong, or to establish new taxa for them.

S. PARADOXUM var. *LONGIPES* Nordstedt 1872
= *S. LONGIPES* (Nordstedt) Teiling 1948.

The essential characters of this desmid, which is now recognised as a good species, are an unornamented body, concave semicell apices

and an acute but very shallow sinus with cuneate or cup-shaped semicells. These characters are excellently typified in the illustrations by NORDSTEDT (1872, fig. 17), WEST and CARTER (1923, Pl. 146, figs. 2—3) and SMITH (1924, Pl. 73, figs. 3—6). Several figures in the literature which have been referred to this taxon are, however, quite different and must be referred elsewhere. These are as follows:

TURNER 1894, Pl. 15, fig. 40 (after WALLICH) Pl. 1, fig. 1.

The biradiate specimens figured by TURNER from India bear no resemblance to NORDSTEDT's desmid and would seem to belong instead to the tetracerum-group of the genus, probably being a form of S. *excavatum*. They should also be compared with S. *tetracerum* var. *cameloides* BRIT-FLORIN (see Pl. 1, fig. 2).

BORGE 1900, fig. 4 forma Pl. 2, fig. 8.

This form with its biundulate apex („forma apicibus semicellularum biundularis") cannot, because of this distinctive character and the shape of the semicell at the isthmus, be accepted as a form of S. *longipes*. These features and its strongly denticulate processes with their stout terminal spines are strongly suggestive of the anatinum-group of the genus and should be compared with S. *bullardii* SMITH and S. *uplandicum* TEILING. In the system of nomenclature for forms of S. *anatinum* suggested by BROOK 1959a, BORGE's form should be named S. *anatinum* f. *longibrachiatum-paradoxum* facies *biradiatum* (cf. also S. *paradoxum* var. *biradiatum* GRIFFITHS in SKUJA 1956, Taf. 38, Fig. 4: Pl. 2, fig. 3).

CARTER 1920, Pl. 14, fig. 30; Pl. 2, fig. 6.

This desmid is much too robust, its processes not sufficiently slender, and its body in the region of the isthmus not of the right shape to be acceptable as a form of S. *longipes*. As with the above it is suggested that this is a form of S. *anatinum* and should be named S. *anatinum* f. *pelagicum-longibrachiatum*.

NYGAARD 1926, Pl. 8, figs. 86—87; Pl. 2, figs. 9.

Again this is probably a desmid of the S. *anatinum*-group, for the body shape is much closer to this than to *longipes* and, moreover, the apex of each semicell is distinctly convex and there is in fact an indication that it is biundulate. It certainly differs very radically from the figures of S. *longipes* in WEST and CARTER 1923 with which it is compared.

FANNING 1901, Pl. 45, fig. 15.

This figure has been commented on by TEILING who considers it to be synonymous with his S. *paradoxum* var. *longibrachiatum*. As will be pointed out later, there is some doubt about the validity of TEILING's variety which certainly bears little resemblance to FANNING's illustra-

tion. The latter in fact seems much more like a form of *S. cingulum*, near the var. *obesum* G. M. Smith.

MARGALEFF 1944. T. iv, fig. 61.

This biradiate form whose semicell shape clearly cannot be referred to *S. longipes* is most probably a form of *S. chaetoceras.*

BEHRE 1956 Taf. 6 fig. 6 (= fa. BORGE 1900) Pl. 2 fig. 5.

The plant figured by BEHRE clearly has affinities with the desmid which BORGE (1900) named as *longipes* (see above). This as stated above belongs to the *anatinum*-group of the genus and according to the nomenclature suggested by BROOK (1959a) should be designated *S. anatinum* f. *longibrachiatum-glabrum-paradoxum,* facies *biradiatum.*

S. *PARADOXUM* var. *OSCEOLENSE* WOLLE 1885, Pl. 1, fig. 3.

The only comment WOLLE (1885, p. 128) makes about this variety is that it „is near the typical form, but much larger, and with the apices of the arms much more prominently forked. Spread of arms 60—70 μ." From these comments, measurements, and very inadequate figures, which WEST and WEST (1896, p. 264) criticised by saying „it does not represent a front view: it is much tilted and incorrectly drawn", it can only be surmised that WOLLE was in fact describing a planktonic, quadriradiate form of *S. anatinum.* However, this is but surmise and in the absence of type material and considering the very inadequate original description, the var. *osceolense* must become a „nomen dubium" and be abandoned. The forms which in the literature have been subsequently referred to this taxon must now be considered:

WEST and WEST 1896 Pl. 17, fig. 9 f. *minor.* Pl. 1 fig. 4.

As already stated, the WESTS expressed doubts about WOLLE's variety and yet it seems that solely on the fact that the small plant which they found possessed large terminal spines they made it a form of this doubtful variety. Since it agrees in so many respects with *S. subgracillimum* which they described and figured in the same paper, it seems very probable that it is merely a form of this species.

GEORGEWITCH 1910, Fig. 6, Pl. 1, fig. 5.

Clearly, on the similarity of the semicell shape in the region of the isthmus, GEORGEWITCH has referred his biradiate desmid to WOLLE's variety. In view of the obviously erroneous impression given by WOLLE's figure even this similarity has no validity. It is quite clear that GEORGEWITCH's plant belongs to the *tetracerum* group of the genus. BRIT-FLORIN (1957) believes it to be synonymous with her *S. tetracerul* var. *cameloides* as is also *S. paradoxum* var. *osceolense* f. *biradiata*

GRÖNBLAD 1944 and *S. osceolense* var. *fennicum* GRÖNBLAD 1948 (see Pl. 1 fig. 2) which should be compared with TURNER's figures of *S. paradoxum* var. *longipes* (Pl. 1 fig. 1).

S. PARADOXUM var. *FUSIFORME* BOLDT 1885, Tab. VI, fig. 37.
= *S. NATATOR* var. *BOLDTII* GRÖNBLAD 1920.

GRÖNBLAD was clearly correct in referring this desmid to *S. natator*. However, it is doubtful whether it is reasonable to maintain the var. *boldtii* which differs from the species merely on the basis of two rings of isthmal granules instead of one. This duplication of granules seems to occur from time to time in the *cingulum*-group of *Staurastrum* to which *S. natator* clearly belongs and in fact dichotypical forms have been observed (BROOK 1959a, Pl. XII, fig. 9). In keeping with TEILING's proposals for the nomenclature of *Staurastrum* species showing different radiation, *S. natator* var. *triquetrum* GRÖNBLAD should become *S. natator* facies *triquetrum* nov. comb.

It is proposed that the var. *boldtii* GRÖNBLAD should be reduced in rank to forma *boldtii* (GRÖNBLAD) nov. comb. for this will simplify the taxonomy of triradiate forms which may be encountered with a double ring of isthmal granules. These will then be referred to as *S. natator*, f. *boldtii* fac. *triquetra*.

S. PARADOXUM var. *CHAETOCERAS* SCHRÖDER in ZACHARIAS 1898
= *S. CHAETOCERAS* (SCHRÖDER) G. M. SMITH 1924. Pl. 2, fig. 1.

In SCHRÖDER's original description of this *Staurastrum* (1898, p. 131), it is first named *S. polymorphum* var. *chaetoceras*. This is presumably an error, for later in the text (p. 132) he refers to „Die neue Varietät von *Staurastrum paradoxum* —".

Some plants referred to this very distinctive desmid are clearly not this species, as for example those drawn by SKUJA 1948, Taf. XIX, figs. 7—8. These very obviously belong to the *anatinum*-group and as stated by FLORIN 1957 come near to *S. uplandicum* TEILING (= *S. alandicum* TEILING). On the other hand several forms which have been named as different taxa must in fact be referred to *S. chaetoceras*. These include *S. paradoxum* var. *biradiatum* GRIFFITHS and probably *S. paradoxum* var. *tosnense* BOLOCHONCEW which will be considered in more detail below. Other figures named as *S. paradoxum* by REYNOLDS (1940), NYGAARD (1945) and COSSANDY (1955) (see BROOK 1959b) should be referred to *S. chaetoceras*. The desmid which FANNING (1901, Pl. 45, fig. 14) ascribes to *S. minneapoliense* is also believed to be a form of *S. chaetoceras*.

S. *PARADOXUM* var. *TOSNENSE* Bolochoncew in Skorikow 1904. Pl. 2 fig. 4.

Florin (1957) in her studies of the plankton of some Swedish waters states that this variety is probably synonymous with S. *longipes* var. *contractum* Teiling. This, however, seems doubtful, for apart from the fact that no biradiate forms of S. *longipes* or its var. *contractum* have yet been found, the shape of the Bolochoncew plant in the region of the isthmus is very different, the sinus being too deep and acute. As Bolochoncew states (p. 389—391) this form has at first sight some resemblance to the var. *chaetoceras* Schröd. (= S. *chaetoceras*). In view of the imperfect description and sketch which accompany it, all that can be admitted is that this desmid is probably a form of S. *chaetoceras* and that S. *paradoxum* var. *tosnense* must be shelved as a „nominum dubium".

S. *PARADOXUM* var. *BIRADIATUM* Griffiths 1925. Pl. 2, fig. 2.

There is little doubt that Griffiths' variety is synonymous with S. *chaetoceras* (see Brook 1959a, p. 600—601). Skuja (1956, Taf. 38, fig. 4) (see Pl. 2 fig. 3) has referred a *Staurastrum* to this variety but this is unquestionably another desmid of the *anatinum*-group, probably synonymous with Teiling's S. *uplandicum*. Clearly S. *paradoxum* var. *biradiatum* cannot be maintained.

S. *PARADOXUM* var. *CINGULUM* West & West 1903
= S. *CINGULUM* (West & West) G. M. Smith

The only doubt about maintaining S. *cingulum* as a separate species rests on the undoubted relationship which exists between this desmid and S. *gracile*, a complete series of forms having been established to connect these two taxa (Brook, 1959a, Pl. XI, figs. 1—14). There is some evidence to suggest that S. *cingulum* is merely the planktonic form of S. *gracile*, but until this has been fully confirmed by experiment, S. *cingulum* cannot as yet be reduced in rank to a variety or form of S. *gracile*.

S. *PARADOXUM* var. *PERORNATUM* Playfair 1912. Pl. 1, fig. 11.

This is a clear example of a desmid which, because it lacks apical ornament has been referred to S. *paradoxum*. This plant, however, would seem to come very close to one or other of the varieties of S. *pseudosebaldii* established by Playfair, i. e. var. *pectinatum* (1908) or var. *corralloideum* (1912). However, until the species S. *pseudosebaldii* can be reinvestigated fully, it is proposed to rename the plant under consideration S. *pseudosebaldii* var. *perornatum* (Playfair) nov. comb.

S. *PARADOXUM* var. *AEQUABILE* Skuja 1956. Pl. 1, figs. 12 and 13.

The shape and dimensions of the cells and the character of the apical and isthmal ornament of Staurastra indicate unquestionably that they are desmids belonging to the *crenulatum-pingue* group of the genus (see Brook 1959a, Pl. XVIII, figs. 1—8). As demonstrated by this author, a series with increasingly long processes has been established connecting *S. crenulatum* and *S. pingue* and indeed it has been suggested (Brook 1959c, Fig. 5) that *pingue* is merely a planktonic form of the benthic *S. crenulatum*. Skuja's var. *aequabile* should also be compared with the illustrations of *S. uniseriatum* (Nygaard 1949, Fig. 57a-e) which is another species of doubtful validity which should at best be reduced in status to a variety of *S. crenulatum*.

S. *PARADOXUM* var. *LONGIBRACHIATUM* Teiling 1946. Pl. 2, fig. 7.

This variety which Teiling clearly established in order to distinguish the more robust Staurastra with long processes and no apical ornament, which occurs in the plankton, from the more delicate and very distinctive *S. longipes*, would appear to be a typical planktonic form of *S. anatinum*. It should be referred to as *S. anatinum* f. *longibrachiatum* - *paradoxum* (see Brook 1959a) (cf. with Pl. 2 figs. 3, 5, 6—9).

S. *PARADOXUM* var. *NODULOSUM* West 1891. Pl. 4, figs. 1—6.

As far as can be ascertained, no subsequent descriptions or illustrations have been published of this small *Staurastrum* described by West from material collected in Upper Lake Killarney, Ireland. The original brief description as „Var. minor apicibus processum leviter trifurcatus; semicellulae a vertice visae triangulares, lateribus binodulosis", and accompanying figure give only a rough impression of this desmid. Through the courtesy of the Keeper of Botany of the British Museum of Natural History, it has been possible to re-examine the West collections of Irish freshwater algae and in these samples a small phial has been found containing squeezings from *Callitriche* from Upper Lake Killarney. A number of small Staurastra are present in this material and amongst these are occasional specimens of a desmid which agrees with West's *S. paradoxum* var. *nodulosum* in size, in the form and disposition of the processes and in the frequently biundulate character of the lateral margins of the semicells when observed in vertical view. West presumably made this desmid a variety of *S. paradoxum* because he observed no ornament on the cell apex, for as stated in a previous paper (Brook, 1959a, p. 604) there has been a tendency to assume that almost any radiate *Staurastrum* with well developed processes, and in which the

apical and sub-apical ornament of the semicell is more or less undiscernible, must be *S. paradoxum,* or a variety of this species.

Critical examination of a considerable number of these *nodulosum* specimens has revealed that they posses important diagnostic characters other than „lateribus binodulosis", and these unmistakably point to a close affinity with *S. micron* West. Most important of these is the angular contour of the semicells in side view (Pl. 4 figs. 1—6), due to the presence of a granule, spine, or in some cases pair of spines on the semicell body above the isthmus. Also important is the occurence of two well developed intramarginal granules or spines on each side of the apex. In fact the biundulate form of the cell margins is associated with the occurrence of this characteristic cell ornament.

In brief, these plants resembly very closely, and can probably be considered synonymous with *S. micron* var. *perpendiculatum* (Grönblad) Brook (cf. Brook 1959d, Pl. 25 (3), figs. 4 + 5)). The length of the processes of the specimens was found to vary considerably, a number being remarkably long, slender and divergent, though frequently they were quite short, so that in effect they closely resembled the species *S. micron.* (Pl. 4, figs. 1, 2 + 4) (cf. *S. paradoxum* var. *parvum,* p. 438 and Pl. 4 figs. 7—8).

S. PARADOXUM var. *EVOLUTUM* West and West 1905.
Pl. 1, figs. 6—9 & Pl. 4 fig. 9.

This small, delicate *Staurastrum* was originally named as a variety of *S. tetracerum* but later, without explanation was referred to the species *S. paradoxum* (West & Carter 1923). The original material from Loch Beosetter, Bressey, in the Shetland Islands has been re-examined. Unfortunately, the bottles containing it have at some time been allowed to dry up and in consequence the contents are in a poor state of preservation. However, the var. *evolutum* is unmistakable in the sample, the shape, dimensions and especially the long delicate processes tipped with very small spines agreeing closely with the West's figures and descriptions. Moreover, the appearance of the plants is immediately suggestive of *S. tetracerum* and there can be little doubt that they should be referred to this species. It is therefore proposed that the original name *S. tetracerum* var. *evolutum* should be revived and replace *S. paradoxum* var. *evolutum.* The forma *biradiata* Moore and Carter of this var. *evolutum* should also be maintained and not renamed *S. exacatum* var. *minimum* as suggested by Nygaard (1926, p. 213). However, in accordance with the proposals of Teiling for desmids showing different degrees of radiation it must become facies *biradiata.*

THOMASSON (1955, p. 220) believes *S. paradoxum* var. *evolutum* to be a variety of *S. longipes* and illustrates in his paper a form which he considers to be intermediate between the species and the var. *contractum* TEILING (see also *S. longipes* var. *evolutum* (WEST & WEST) THOMASSON in THOMASSON 1959, Fig. 23, 10—11). *S. longipes*, however, is a much larger desmid than the variety in question and there would appear to be no close relationship between these two taxa so that THOMASSON's suggested change in nomenclature cannot be accepted.

It should be pointed out with regard to *S. tetracerum* var. *evolutum* that in WEST and CARTER (1923, p. 107) the impression is given that it occurs generally in the plankton of the Shetlands. However, before the WEST's original material was obtained, plankton samples collected during the Bathymetrical Survey and known to have been examined by the WESTS (WEST & WEST 1905) were worked through. In these collections *S. pingue* TEILING occured in 8 out of the 9 lochs sampled and since the WESTS only reference to a small bodied desmid with long slender processes was the desmid which they named *S. paradoxum* var. *evolutum*, it was assumed, though incorrectly, that the latter was synonymous with *S. pingue* (BROOK 1959a, p. 603). The present study however, has shown that they are quite distinct and that of these two small bodied radiate Staurastra, only *S. pingue* is common and widely distributed in the plankton of the Shetland Islands.

S. PARADOXUM var. *PARVUM* WEST 1892. Pl. 3, figs. 1—11.

Of the numerous varieties referred to *S. paradoxum*, the var. *parvum* has become the most vague and indeed almost as large a dumping ground as *S. paradoxum* itself. Thus it would seem that any very small *Staurastrum* without distinct semicell ornament has been given this name. However, a collection of some of the published figures (Pl. 3, figs. 1—11) shows clearly how greatly algologist's interpretations of WEST's variety differ. This confusion over the identity of the var. *parvum* is not really surprising when the vagueness and confusion surrounding the now-abandoned species *paradoxum* itself is considered and an attempt is made to try to relate the var. *parvum* to it, for in what is undoubtedly the most widely used monograph on the genus *Staurastrum* (WEST & CARTER 1923), this variety is typified by the brief description — „cells similar to type but exceedingly minute". Identification is not helped by the figure accompanying this description, and to add to the confusion, this figure differs from that published when the variety (as f. *parva)* was first described (WEST 1891). Pl. 145 fig. 6 in WEST and CARTER's monograph shows a plant in which the angles of one semicell alternate with those of the other, a character which is

not mentitoned in the original description or shown in the figure accompanying it.

In the WESTS' Irish Collection a phial has been found containing material from Adrigole, one of the localities from which West first described his f. *parva*. This sample, rich in small benthic desmids, is clearly of material squeezed from aquatic plants and the small *Staurastrum* named S. *paradoxum* f. *parva* by WEST is without doubt present in fair numbers. Their appearance under the low power (1/2 in. objective) of the microscope agrees well with the ‚impression' provided by WEST's original figure. This latter, however, is quite lacking in detail, but the material itself when looked at under higher power can be seen to bear the distinctive characters of S. *micron*. It has already been pointed out that S. *paradoxum* var. *nodulosum* is synonymous with S. *micron* var. *perpendiculatum* and with this in mind it is instructive to compare WESTS figures representing his f. *parva* and var. *nodulosum* of S. *paradoxum* (WEST 1891, pl. 23, figs. 12 + 13). Even WEST's somewhat sketchy figures indicate a fairly close affinity between these two taxa. Moreover, it will be remembered that many specimens of S. *micron* var. *perpendiculatum* (= S. *paradoxum* var. *nodulosum)* in the original sample from Upper Lake Killarney approach the species S. *micron* very closely.

Of the published figures referred to S. *paradoxum* var. *parvum* (Pl. 4, figs. 1—11), only those of BORGE 1936 and PRESCOTT 1940 (figs. 3 and 8 respectively) would seem to agree with that must now be taken as the type material, that is the Adrigole specimens now referred to S. *micron*. The others are of quite distinct taxa which it does not seem possible to place with any degree of certainty.

SUMMARY

The following varieties of S. *paradoxum* have been considered from the point of view of their taxonomic relationships, and as a result, most can either be maintained as distinct species, as certain authors have already suggested, or they must become varieties of other well established species. The only varieties of S. *paradoxum* which cannot be so placed are WOLLE's inadequately described and figured var. *osceolense* and TURNER's var. *depressum* which must become „nomina dubia" and abandoned, though the var. *tosnense* is also very doubtful and must be similarly shelved. The proposed nomenclature for these varieties is given below:

1. var. *longipes* NORDST 1872 = S. *longipes* (NORDST.) TEILING
2. var. *osceolense* WOLLE 1885 = „nomen dubium"
3. var. *fusiforme* BOLDT 1885 = S. *natator* forma *boldtii* (GRÖNBLAD) BROOK nov. comb.

4. var. *nodulosum* West 1892	= *S. micron* var. *perpendiculatum* (Grönblad) Brook
5. var. *depressum* Turner 1892	= „nomen dubium"
6. var. *parvum* West 1892	= *S. micron* West forma
7. var. *Chaetoceras* Schröder in Zacharias 1898	= *S. chaetoceras* (Schröd.) G. M. Smith
8. var. *cingulum* West & West 1903	= *S. cingulum* (West & West) G. M. Smith
9. var. *tosnense* Boloch. in Skorikow 1904	= „nomen dubium" but probably a form of *S. chaetoceras.*
10. var. *evolutum* West & West in West and Carter 1923	= *S. tetracerum* var. *evolutum* West & West 1905 „nomen resucitatum"
11. var. *perornatum* Playfair 1912	= *S. pseudosebaldii* var. *perornatum* (Playf.) Brook nov. comb.
12. var. *biradiatum* Griffiths 1926	= *S. chaetoceras* (Schröd.) G. M. Smith
13. var. *longibrachiatum* Teiling 1946	= *S. anatinum* f. *longibrachiatum* - *paradoxum* Brook
14. var. *aequabile* Skuja 1956	= *S. pingue* Teiling, near *S. crenulatum* (Näg.) Delp.

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EXPLANATION OF THE PLATES

Plate (1)

Fig. 1. *S. paradoxum* var. *longipes* after TURNER 1894.
Fig. 2. var. *longipes* after SKORIKOW 1904.
Fig. 3. var. *osceolense* after WOLLE 1885.
Fig. 4. var. *osceolense* after WEST & WEST 1896.
Fig. 5. var. *osceolense* after GEORGEWITCH 1910.
Fig. 6 & 7. var. *evolutum* after WEST & WEST 1905.
Fig. 8. var. *evolutum* after LIND 1952.
Fig. 9. var. *evolutum* f. *biradiatum* after MOORE & CARTER 1923.
Fig. 10. *S. longipes* var. *evolutum* after THOMASSON 1955.
Fig. 11. var. *perornatum* after PLAYFAIR 1912.
Figs. 12 & 13. var. *aequabile* after SKUJA 1956.
Fig. 14. var. *depressum* after TURNER 1892.

Plate (2).

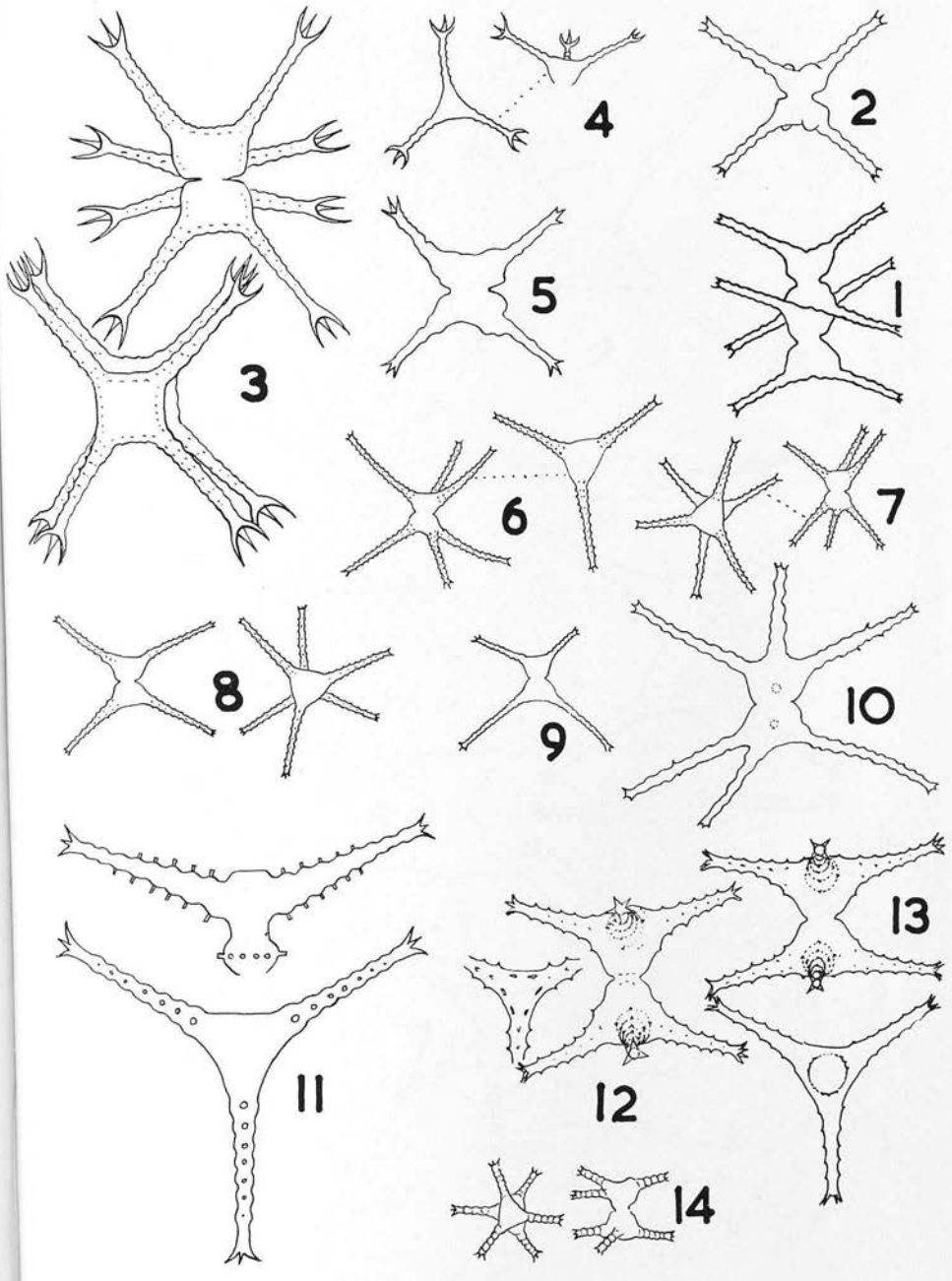
Fig. 1. var. *chaetoceras* after SCHRÖDER in ZACHARIAS 1898.
Fig. 2. var. *biradiatum* after GRIFFITHS 1925.
Fig. 3. var. *biradiatum* after SKUJA 1956.
Fig. 4. var. *tosnense* after BOLOCHONCEW in SKORIKOW 1904.
Fig. 5. var. *longipes* f. BORGE after BEHRE 1956.
Fig. 6. var. *longipes* after CARTER 1920.
Fig. 7. var. *longibrachiatum* after TEILING 1946.
Fig. 8. var. *longipes* after BORGE 1900.
Fig. 9. var. *longipes* after NYGAARD 1926.

Plate (3) Figures representing *S. paradoxum* var. *parvum.*

Fig. 1. after WEST 1892.
Fig. 2. after SKVORTZOW 1932.
Fig. 3. after BORGE 1936.
Fig. 4. after SKUJA 1956.
Fig. 5. after SCHMIDLE 1895.
Fig. 6. after THOMASSON 1955.
Fig. 7. after MESSIKOMMER 1955.
Fig. 8. after PRESCOTT 1940.
Figs. 9—11. after SMITH 1924.
Fig. 12. after PRESCOTT and SCOTT 1942.

Plate (4).

Figs. 1—6 *S. micron* var. *perpendiculatum* (GRÖNBLAD) BROOK (= *paradoxum* var. *nodulosum* WEST) drawn from type material from upper Lake Killarnay.
Figs. 7—8 *S. micron* WEST forma (= *S. paradoxum* var. *parvum)* drawn from type material from Adrigole, Ireland.
Fig. 9. *S. tetracerum* var. *evolutum* WEST & WEST (*S. paradoxum* var. *evolutum* WEST & WEST) drawn from type material from Loch Beosetter, Shetland.
Fig. 10. *S. longipes* (NORDST.) TEILING from Lough Ballynahinch, Ireland, clearly indicating the much greater size of this species compared with *S. tetracerum* var. *evolutum.*



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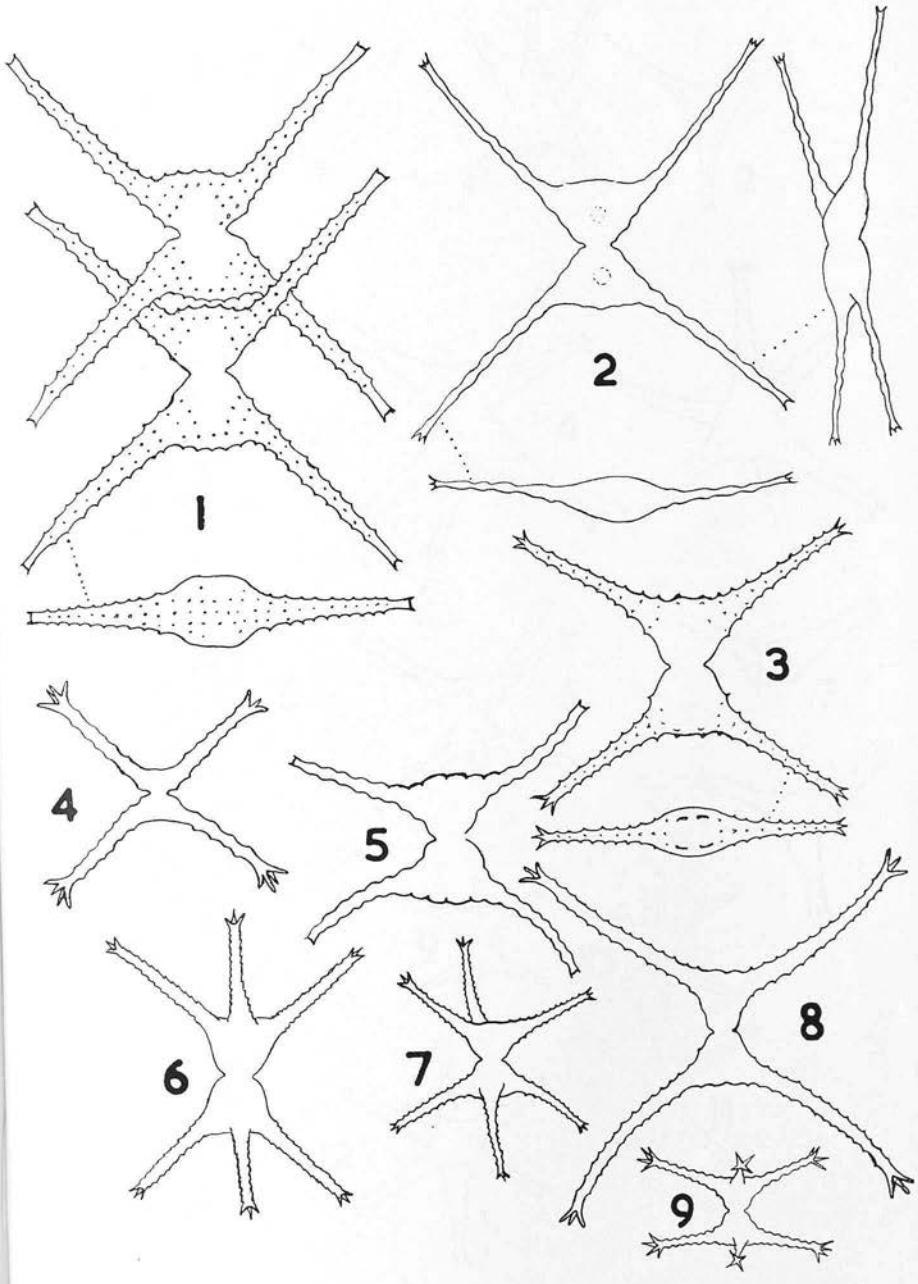

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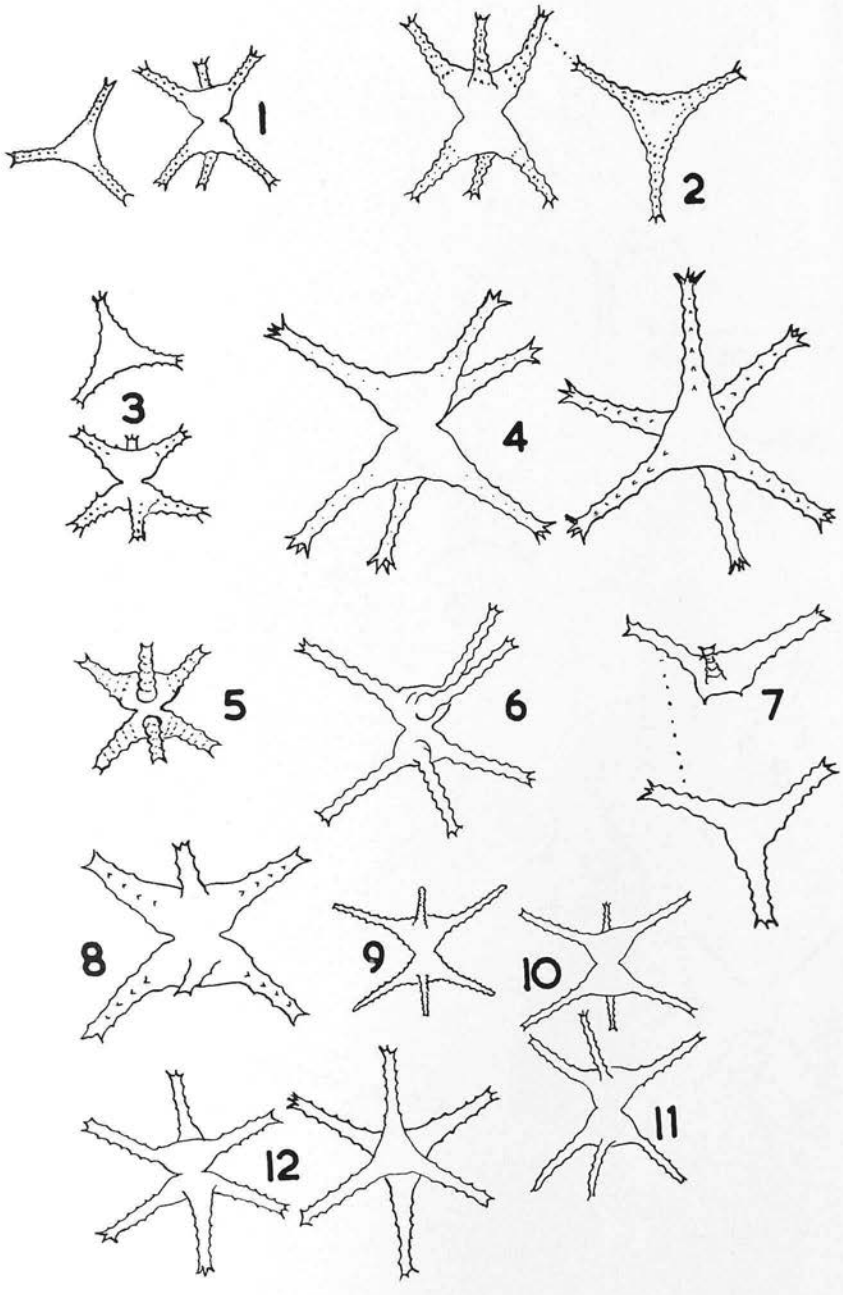

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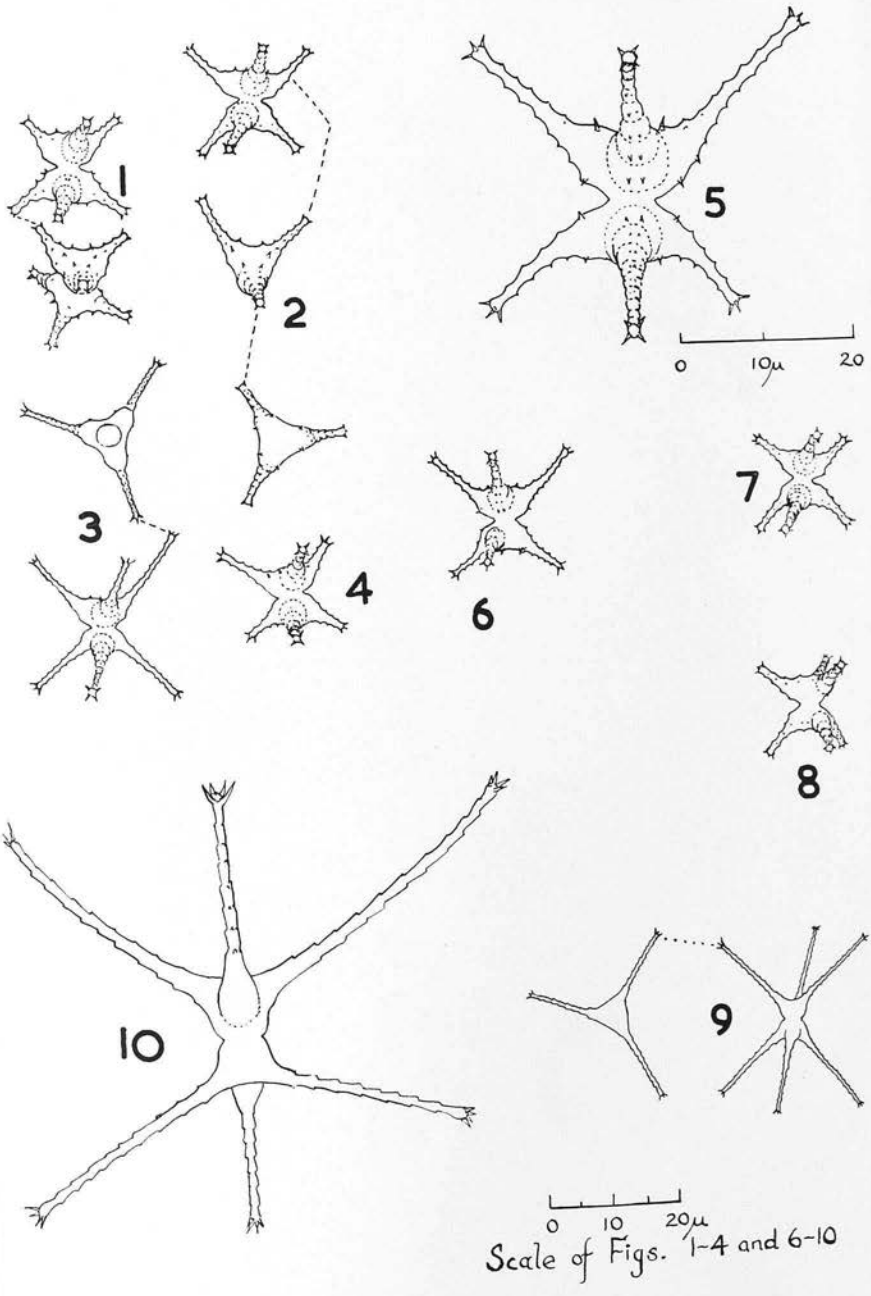

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22

NOTES ON DESMIDS OF THE GENUS *STAURASTRUM* I

BY

A. J. BROOK

(*Reprinted from 'The Naturalist,' July-September, 1957*)

A. BROWN & SONS, LIMITED
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NOTES ON DESMIDS OF THE GENUS *STAURASTRUM*

I. *STAURASTRUM PSEUDOPELAGICUM, S. SUBCRUCIATUM, S. AVICULA* AND *S. DENTICULATUM*

A. J. BROOK

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Staurastrum pseudopelagicum W. & G. S. West in J. Linn. Soc. Bot., **35,** 547, Pl. 18, figs. 1-3, 1903. (Figs. 1-7.)

In commenting on the forms of this desmid occurring in the Wisconsin lakes, Smith (1924, p. 83) states that these have a less stout body than those in the original illustrations of this species from British material, made by the Wests (West and Carter, 1923, Pl. 145, figs. 11-12). Most, if not all of the figures of this desmid published since 1924 seem to have been of stout bodied forms (Skuja 1949, Irénée-Marie 1952, Thomasson 1952, Brook 1955), a fact which rather suggests that the Wisconsin forms are atypical, though Smith (*loc. cit.*) does state that the more delicate forms he has figured also occur in collections which he has examined from Loch Morar, Scotland. My own observations on this desmid, which is widely distributed but never seems to be abundant in the plankton of oligo- and mesotrophic lakes throughout the British Isles, have indicated that the semicells and their processes may vary considerably in shape and robustness. At one extreme there are the very tumid forms with short, stout processes such as occur in Loch Shurrery, Caithness (Fig. 1), intermediate types with more elongated and delicate processes from Loch Katrine and Loch Tay (Figs. 2-3), and the more flattened, slender forms, similar to Smith's figures, which occur at times in Windermere (Fig. 4).

Several investigators have commented on the variability in the number of the stout diverging spines with which the processes of this *Staurastrum* are tipped. Most frequently there are two, lying vertically one above the other (see West and Carter, p. 107), though Smith's American plants have three as the most frequent number. Less commonly specimens with the processes in one semicell bearing two spines, and in the other three may occur (Brook 1955, also Fig. 1). Recently I have seen a number of specimens from Windermere in which one or more, and sometimes all of the processes are tipped with only one spine (Fig. 5). It will be seen that the unusual form figured here from Loch Achray bears four spines on several of its processes (Fig. 6).

The ornamentation of the semicells is also a character subject to considerable variation, though basically it consists of rings of small granules arranged in concentric series round the processes, continuing onto the semicell body. These granulations may be very distinct, irregular or almost invisible. On the apex and sides of the body the granules tend to be much less prominent than on the processes and apparently less regular in their disposition, this apparent irregularity probably being due to their uneven development. On the apex of each semicell, it is possible to distinguish three pairs of granules, more prominent than the rest (Fig. 1, vertical view), near the point of origin of each process. Very frequently, some (Fig. 7) or all of these granules may be so enlarged that they constitute spines of considerable length (Figs. 3, 4 and 6). Thomasson (1952, p. 236, fig. 6) has described a variety of *S. pseudopelagicum* which he has named var. *spinosa*, largely on account of the delicate spines which he found occurring on the semicell apices in the position described above. Smith's var. *tumidum* of this species (Smith 1924, p. 84, Pl. 72, figs. 8-11) bears similar, though less well developed apical spines. Thomasson states that his variety differs from the latter in its better developed spines, shorter processes and more compact shape of the semicells. Since, however, all of these characters seem very variable and one can find all combinations of body shape, process length and development of apical spines (indeed Thomasson's desmid seems to be more tumid than Smith's var. *tumidum*, especially in the greater curvature of the cell apex), it seems doubtful whether these two varieties can reasonably be maintained. It is suggested that it would be better to reduce them to the status of forms, though even if this is done one is still faced with the problem of putting a name to distinctly slender forms with apical spines, or decidedly tumid forms without them.

Smith (*loc. cit.*) states that *S. pseudopelagicum* should be compared with *S. lacustre* G. M. Smith, and some of the British specimens of the former species seem to show an even greater similarity with the latter species than do Smith's Wisconsin plants. In Figs. 2 and 6, the processes are very slender and considerably elongated and their

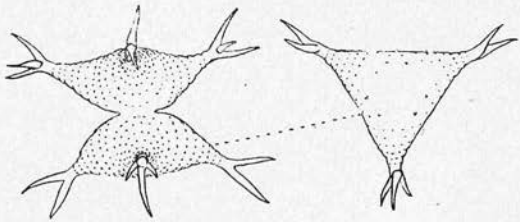

FIG. 1

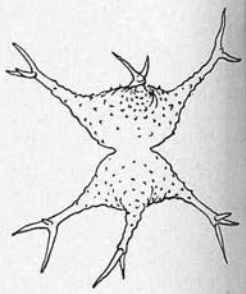

FIG. 2

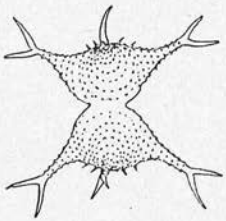

FIG. 3

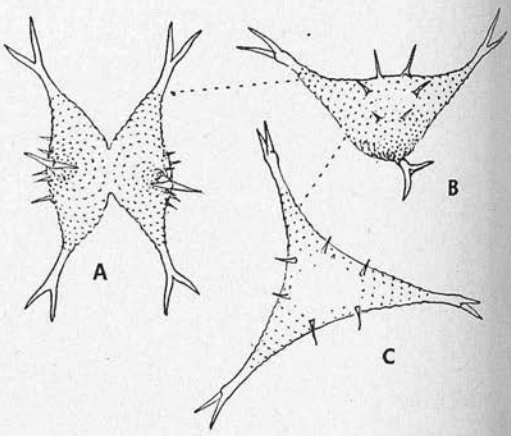

FIG. 4

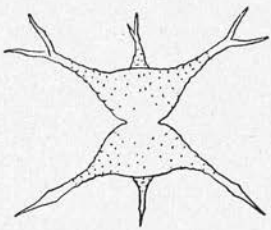

FIG. 5

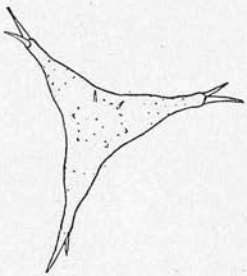

FIG. 7

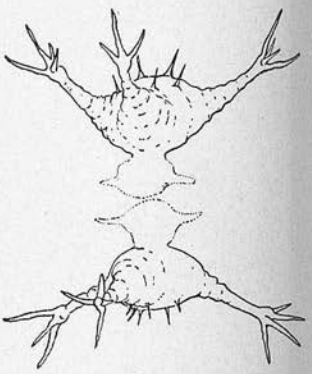

FIG. 6

FIGS. 1-7. *Staurastrum pseudopelagicum* W. and G. S. West. × 500

granular ornamentation much reduced (see also Fig. 7), while the apical ornamentation differs only in that *S. pseudopelagicum* bears spines and *S. lacustre* verrucae. With reference to this latter character, it is now generally recognised that granules, spines and verrucae represent different degrees in the development of the same ornament, a fact which is emphasised by Irénée-Marie's drawing of the vertical view of *S. lacustre* from Canadian material (Irénée-Marie 1939, Pl. 59, fig. 2) in which spines do in fact occur on the apex. The major difference in these two species would thus seem to be in the restriction of the ornamenting granules to the processes in *S. lacustre*, and in the shape of the semicell body which is more robust and tumid in *S. pseudopelagicum*. However, even these characters tend to converge in the two species (compare especially Smith 1922, Pl. 12, figs. 13-15, and West and Carter 1923, Pl. 145, fig. 11).

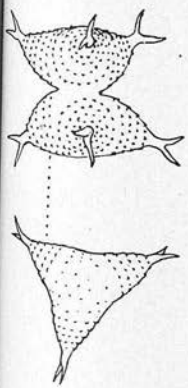

FIG. 8. *S. subcruciatum* Cooke and Wills × 500

S. subcruciatum Cooke and Wills in Brit. Desm., 148, Pl. 51, fig. 3, 1887. (Fig. 8.)

There is no suggestion in West and Carter's monograph on the genus *Staurastrum* (West and Carter 1923) of any affinity between *S. subcruciatum* and *S. pseudopelagicum*, though an affinity seems to be implied between the former species and *S. avicula* Bréb. through the var. *subarcuatum* West, from which it is stated to be distinguished by 'its finer granulation and by the fact that the angles of the semicell are produced to form distinct cylindrical processes.' The specimen of this desmid from Lochan Daimh Mhor, Sutherland, figured here (Fig. 8), and those in West and Carter (Pl. 133, Figs. 6-7) do, however, clearly suggest a relationship with *S. pseudopelagicum*. Indeed, *S. subcruciatum* may perhaps be regarded as a robust (benthic ?) form of the latter species with much reduced processes, for the shape and dimensions of the semicell body, the ornamentation, and the stout, divergent forked spines with which the processes are tipped, are characters common to both.

S. avicula Bréb. in Ralfs Brit. Desm., 140, Pl. 23, fig. 11, 1848, forma (Fig. 9.)

A hitherto undescribed form of *S. avicula* differing most radically from type in possessing six delicate spines on the apex of each semicell which are identical in appearance and their disposition with those occurring in *S. pseudopelagicum* has been found on rare occasions in the plankton of Ennerdale Water. These plants are, however, very similar to the desmid named *S. avicula* var. *tyrolense* Schmidle by Irénée-Marie (1939, Pl. 55, fig. 5), though differing in that the apical ornament is shown as verrucae. Also similar is the *Staurastrum* which Huber-Pestalozzi (1928, Taf. 13, fig. 11) has described from Corsica and named var. *granulato-furcigerum* of *S. forficulatum* Lund. This desmid seems to bear only the most superficial resemblance to the latter species and it is suggested that it is probably much more closely related to this Ennerdale desmid. *S. arcuatum* var. *guilanense* West would seem to be another closely related form.

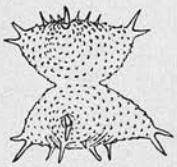

FIG. 9. *S. avicula* Bréb. forma × 500

With regard to the shape of the semicells, this Ennerdale form of *S. avicula* comes nearer to the var. *subarcuatum* than to the species itself. The cell wall, as in the type, is covered with minute granules arranged in concentric series round the angles and progressively reduced in prominence centripetally, while the tips of the stout angles are furnished with two spines, much more robust than in the type, placed vertically one above the other.

S. denticulatum (Naeg.) Arch. in Pritch. Inf., 738, 1861. (Figs. 10-12.)

In the restriction of the concentric rings of granules to the angles of the semicells, none being present in the central region, this species would seem to bear a similar relationship to *S. avicula* as *S. lacustre* does to *S. pseudopelagicum* (see above). Some unusual forms of this desmid, which does not appear to have been previously recorded from Scotland, have been found from time to time in the plankton of

Loch Mhullaich, Sutherland. Of these, the most remarkable were those in which one semicell was more or less typical while in the other, the angles were rounded and considerably reduced and devoid of granular ornamentation and the paired spines normally tipping them (Fig. 10 A-C). In general appearance these aberrant semicells bear a strong resemblance to those of *S. subpygmaeum* West, though they are somewhat smaller. Intermediate forms between this condition and the normal have also been observed and should be compared with *S. trachytithophorum* W. and G. S. West. The semicells in these specimens (Fig. 11) are more broadly triangular in vertical

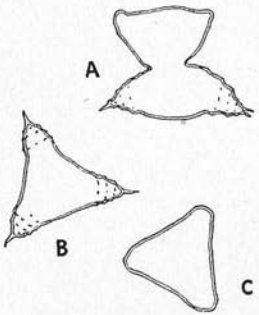

FIG. 10.

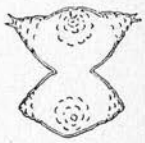

FIG. 11.

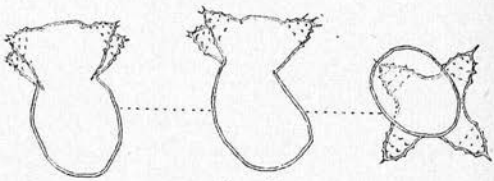

FIG. 12

FIGS. 10-12. *S. denticulatum* (Naeg.) Arch. × 500

view than in the typical form and the paired spines which usually tip them are again absent, though the granular rings round the angles are still apparent.

Even more aberrant than the above forms are the occasional specimens, some triradiate and a few quadriradiate (Fig. 12), in which one semicell has the form of an asymmetrical and elongate sac, bearing no resemblance at all to the adjoining, normal semicell.

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NOTES ON DESMIDS OF THE GENUS *STAURASTRUM* II

BY
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NOTES ON DESMIDS OF THE GENUS *STAURASTRUM*

II. *STAURASTRUM LEPTODERMUM*, *S. LONGISPINUM*, *S. BRASILIENSE*, *S. SETIGERUM*, *S. CLEVEI* and *S. TOHOPEKALIGENSE* var. *TRIFURCATUM*

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S. leptodermum Lund. in *Nova Acta Soc. Sci. Upsal.*, 8, Pl. 3, Fig. 26, 1871 (Figs. 1-3).

There is only one previous record of this desmid for the British Isles, this being from Slewdrum, Aberdeenshire (Roy and Bissett, 1893, p. 239). Recently, however, it has been found in small numbers in the plankton of Loch na Beiste Brice, and Dar Loch, Sutherland, and in considerable amounts in Loch Morlich, Inverness. Basically, the semicells may be regarded as more or less spherical, the sides and apex of each being broadly rounded. In vertical view it would appear that a triangular shape has been implanted on the spherical body by the production of three mammillate processes of variable length, each of which is usually tipped with a characteristic short spine, both spines and processes in side view being directed obliquely upwards. Quite frequently specimens have been found in which these short spines are absent (see Figs. 2 and 3 lower semicells) in which condition the semicells are then indistinguishable from those of *S. subpygmaeum* West (West, 1892) which would thus only seem to be a form of *S. leptodermum*. Additional weight is given to this belief by the fact that both "species" have the same size range, both have finely punctate cell walls (Fig. 2) and both are frequently enveloped in a wide gelatinous integument (Fig. 3). It is therefore proposed that these two species should be combined, and since *S. leptodermum* was the first to be described, this name should be retained. It is suggested that specimens without spines tipping their processes should be referred to as forma *subpygmaeum* (West) nov. comb of *S. leptodermum*. The var. *subangulatum* West and Carter (1923) of *S. subpygmaeum* must be abandoned.

S. longispinum (Bail.) Arch. in *Pritch. Inf.*, p. 743, 1861 (Figs. 4-6).

This species is of frequent occurrence in the plankton of oligotrophic lakes throughout the British Isles and whilst most of the semicell characters are quite constant, there is a very considerable variation in the length of the pairs of stout spines which normally terminate the very slightly produced angles of the semicells. Most commonly their length is from 15-25μ though occasionally specimens have been found in which these spines have been as long as 45μ (Fig. 4). At the other extreme they may be reduced to almost wart-like protuberances of less than 5μ in length and, moreover, considerable differences in length may be found in adjoining semicells (Fig. 5). Thus the maintenance of the var. *bidentatum* (Wittr.) West and West which is separated from the type species only by the possession of very short spines does not seem warranted.

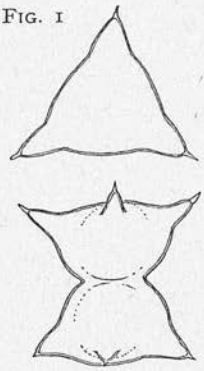
On occasions (Fig. 6) individuals have been seen in which some or all of the angles of the semicell have been tipped with three spines.

S. brasiliense Nordst. in *Vidensk. Medd. Dansk Naturh. Foren. Kbh.*, Nos. 14-15, p. 227, Pl. 4, Fig. 39, 1869 (Figs. 7-9).

Only the var. *lundellii* West and West of this large planktonic desmid has been previously recorded from Britain though this often occurs in abundance in oligotrophic lakes. In a plankton sample from Loch Morlich, Inverness-shire, however, many specimens have been found which must be referred to the species, being four-angled in vertical view, the angles terminating typically in three stout diverging spines. In occasional specimens, four spines have been observed at some or all of the angles (Fig. 7) caused by the duplication of the middle, upwardly directed spines. In other specimens, some of the spines may be bi- or even tri-furcate (Fig. 8). The sides of the cells were less concave and the angles not so prominently produced as in the specimens figured by Nordstedt and therefore had a more square and robust appearance.

In accordance with Teiling's valuable proposals (1950) concerning the nomenclature of those desmid species which show diversity in their radiation, pentagonal forms, previously referred to as the var. *lundellii*, should now be named *S. brasiliense* forma *lundellii*. Such forms occurred as frequently as the type species in Loch

FIG. 1



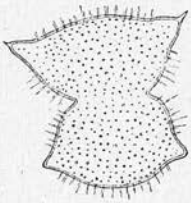


FIG. 2

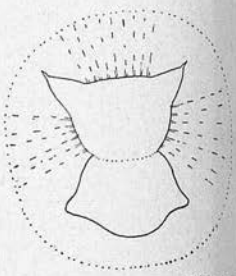


FIG. 3

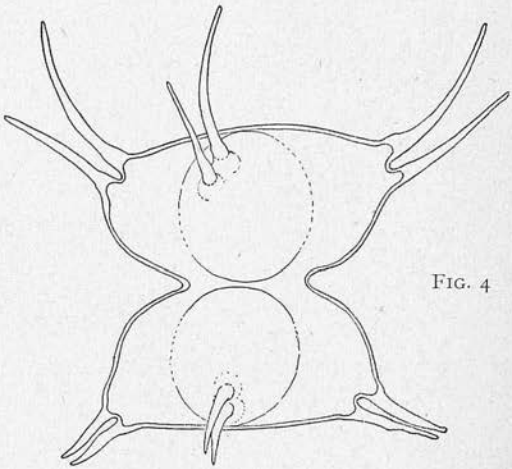


FIG. 4

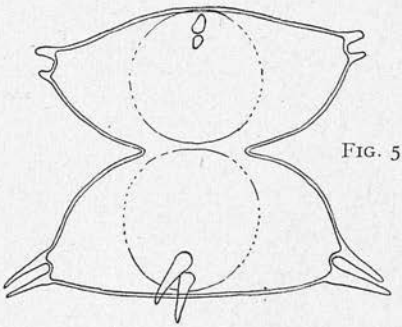


FIG. 5

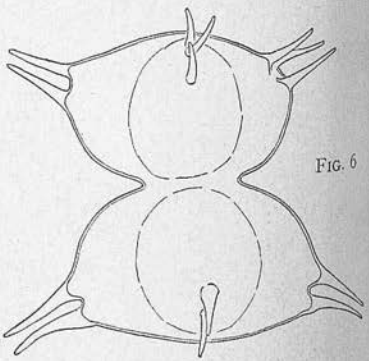


FIG. 6

FIG. 1–3. *S. leptodermum* Lund. × 450.

FIG. 4–6. *S. longispinum* (Bail.) Arch. × 450.

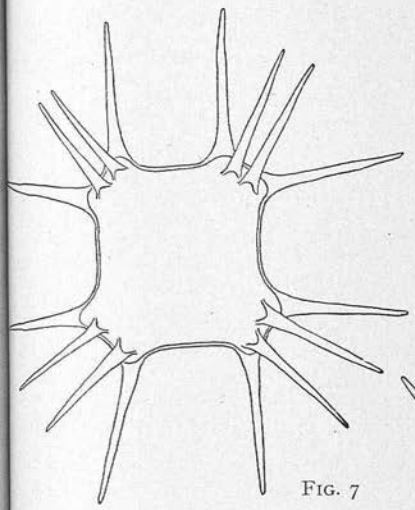


FIG. 7

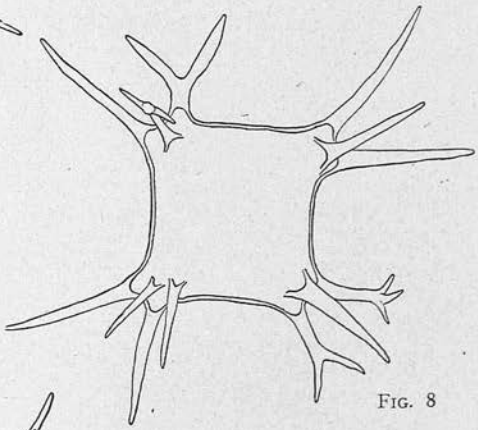


FIG. 8

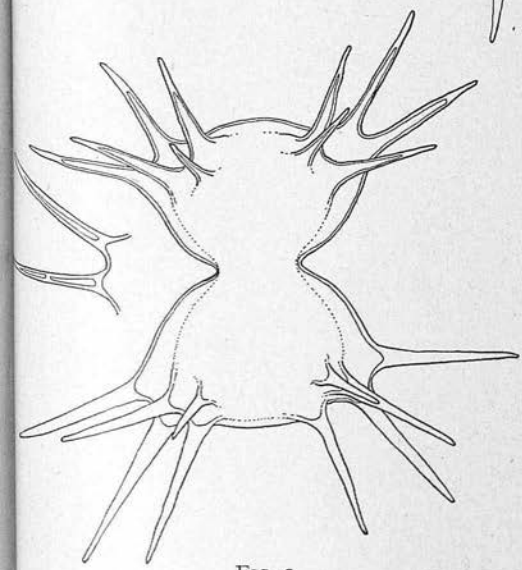


FIG. 9

FIG. 7–9. *S. brasiliense* Nordst. × 450.

Morlich though these again differed from the specimens figured in West and Carter (1923, Pl. 135, Figs. 12-13) in that the sides and apices of the semicells were distinctly convex instead of being almost straight. In addition, many of the spines were hollow instead of being solid (see upper semicell in Fig. 9).

S. setigerum Cleve in *Ofvers. Vetensk. Acad. Forh., Stockh.*, No. 10, p. 490, Pl. 4, Fig. 4, 1864 (Fig. 10).

The figures depicting this species in West and Carter (1923, Pl. 136, Figs. 13-14) do not represent this species adequately. The most important omission from their figures is that they do not show that the angles of the triradiate semicells are slightly produced as in the case of *S. longispinum* and though they show the angles to be tipped with from two to five (usually three) long, gracefully-tapering spines, they do not indicate that the upper one at each angle is usually longer than the others

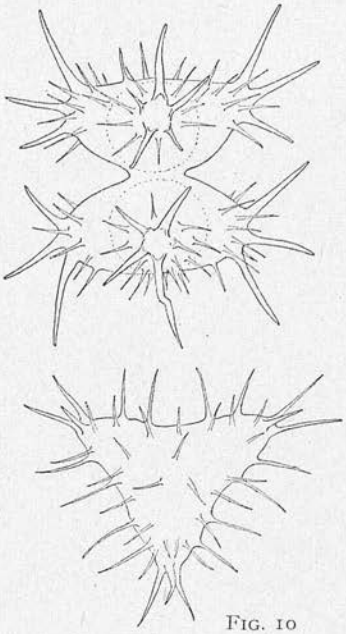


FIG. 10

FIG. 10. *S. setigerum* Cleve. × 450.

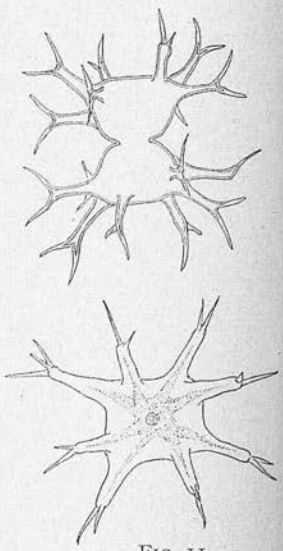


FIG. 11

FIG. 11. *S. clevei* (Wittr.) Roy and Biss. × 450.

and directed upwards, almost at right angles to the semicell apex which in addition tends to be much less convex than is shown in their figure.

S. clevei (Wittr.) Roy and Biss. in *Ann. Scot Nat. Hist.*, 1893, p. 18, facies *quadriradiata* fac. nov. (Fig. 11).

There appear to be no previous records of quadriradiate forms of this rare plankton desmid, a few specimens of which have now been found in a plankton sample collected in September 1953 by Dr. F. Hustedt from Loch na Achlaise, Perthshire (Hustedt, 1954, p. 272). These quadriradiate forms differ from the typical triradiate forms only in that in vertical view the semicells are quadrate with their sides more or less straight instead of being somewhat convex. As in the species, an apical accessory process arises on the right side of each angle of the semicell, projecting obliquely upwards and forming an angle of 30° with the lower process when viewed vertically (Fig. 11b). Like the lower whorl of processes these accessory processes are deeply bifid their slender spines lying above one another in the same plane. Occasionally some of the processes may be trifid. This fac. *quadriradiata* of

S. clevei could be confused with *S. tohopekaligense* Wolle, from which it is principally distinguished by the possession of only a single, instead of a pair of accessory processes on the apex at each angle.

S. tohopekaligense fac. *trifurcatum* (W. & G. S. West) stat. nov. (=var. *trifurcatum* W. & G. S. West in *Trans. Linn. Soc. Bot.*, **5**, p. 80, Pl. 9, Fig. 8, 1895) Fig. 12.

As in the case of *S. brasiliense* var. *lundellii* (see above) the nomenclature of this triradiate form of *S. tohopekaligense* has been modified in accordance with the proposals of Teiling (1950). Like *S. clevei* it is a rare 'Western' type of plankton

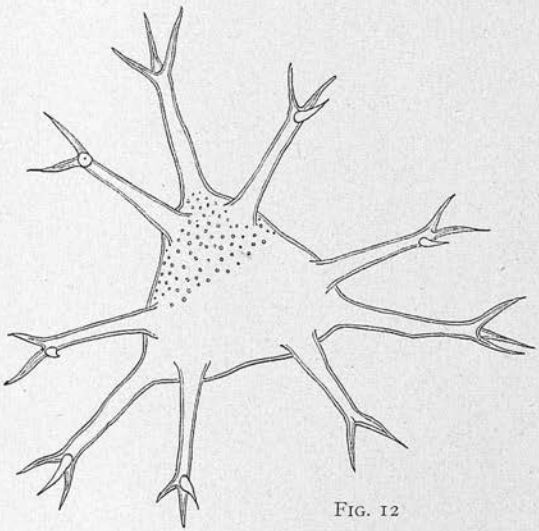


FIG. 12

FIG. 12. *S. tohopekaligense* fac. *trifurcatum* (W. & G. S. West). × 800

desmid and has previously been recorded in Britain from only one locality in Sutherland and one in Lewis. Recently, however, occasional specimens have been found in some lochs in the Trossachs region of Perthshire. In these, both the upper and lower series of processes were longer and more slender than those depicted by West and West (1905, Pl. 7, Fig. 7) from Scottish plankton. Some of the Perthshire specimens were examined under an oil immersion objective and it was observed that the semicell wall, stated in West and Carter (1923, p. 178) to be smooth, was very finely and evenly punctate (Fig. 11).

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STAURASTRUM PENDULUM var. *PINGUIFORME* CROASDALE, *S. MINOR* WEST f. *MAJOR* f. nov., fac. *QUADRATA* and *S. MICRON* var. *PERPENDICULATUM* (GRÖNBLAD) nov. comb., desmids new to the British Freshwater plankton.

by A. J. BROOK, Edinburgh.

With plate 25 (1) — 27 (3).

STAURASTRUM PENDULUM var. *PINGUIFORME* CROASDALE.

Often conspicuous in the net plankton of both oligotrophic and eutrophic lakes are one or more species of desmids of the genus *Staurastrum*. These usually possess small bodies lacking in prominent ornamentation, and have long divergent processes (see pl. 25 (1), fig. 20 and 22). Reference to the literature shows that such typical plankters have been referred most frequently to one or other of two vaguely described ‚rubbish-dump' species, *Staurastrum paradoxum* MEYEN, or *S. gracile* RALFS (BROOK 1959 a). Recently a detailed study of such forms has been made with special reference to the British freshwater plankton (BROOK 1959b) and an attempt made to refer the considerable range of forms encountered to more firmly established taxa. As a result, most of the forms possessing these characters in plankton samples from over 300 lakes have been identified. One exception, however, is a *Staurastrum* predominant at times in the net plankton of a series of large, deep, glacial lakes (Lochs Ericht, Eagheach, Rannoch and Tummel) which feed the River Tummel, a tributary of the River Tay (pl. 25 [1]). These plants were tentatively recorded as forms of *S. paradoxum* var. *evolutum*, described by WEST and WEST (1905) from lochs in the Shetland Islands. Although somewhat larger in size, the Tummel desmids show several similarities, the most striking of which is the cell shape in side view and the invariable twisting of the cells at the isthmus, so that in apical view, the angles of one semicell alternate with those of the other (pl. 25 [1], fig. 21). They differ from *S. paradoxum* var. *evolutum*, however, in that the sides of the semicells do not appear markedly convex in apical view, and in that they possess a distinctive apical ornamentation which is neither described nor figured by the WESTS. This consists of

either a single, or double, series of 9 intramarginal granules in rows of 3 within each side of the apex, and 6 regularly arranged minute mucilage pores in the central area (pl. 25 [1], fig. 8, 15, 18, 21). The character and arrangement of the apical granules, coupled with the shape and isthmal twisting of the semicells points to these desmids being forms of *S. pendulum* NYGAARD, a species first described and indeed to date recorded from only one locality in Denmark (NYGAARD 1949). A variety, var. *pinguiforme* has recently been described from an Alaskan lake (CROASDALE 1958).

The cell measurements are of the same order as for the species and the variety, being 22—27 μ long (sine pro.) and 6—7 μ brd. at the isthmus. The processes of the Scottish plants are however, considerably longer than in the species, making the overall breadth, including the processes from 65—72 μ in most cases, and thus similar to the var. *pinguiforme*. The processes are in addition more slender and graceful, as are also the three or four terminal spines with which they are tipped. Moreover, the processes are more strongly divergent than in the Danish forms and only a small proportion show any tendency to converge near their extremities (see pl. 25 [1], fig. 9 and 22).

With regard to what is probably the most important diagnostic feature, the apical ornament, this agrees fairly well with NYGAARD's description, though as pointed out by CROASDALE with regard to the Alaskan material, it shows considerable variation. The inner series of intramarginal granules on the apex may occur as granules, spines, 'granula bigemina' (pl. 25 [1], fig. 8) or exceptionally as 'verrucae' (see aberrant lower semicell in pl. 25 [1], fig. 12) and in various combinations (pl. 25 [1], fig. 8, 15—18 and 21). Thus the central granule along each side may be enlarged as a prominent spine (pl. 25 [1], fig. 18), or it may occur as a very small granule and the outer granules of each series of three may occur as spines (pl. 25 [1], fig. 17). In the majority of cases, however, the apical decoration is extremely delicate and can only be seen clearly in empty cells (pl. 25 [1], fig. 15). Furthermore, the outer of the two parallel series of granules shown in some of NYGAARD's figures of *S. pendulum* cannot always be discerned, which also seems to have been the case with the Alaskan plants described by CROASDALE.

Consideration of the character of the Scottish plants with those of the species and the var. *pinguiforme*, suggests that they should be referred to the latter. With reference to the relationship of *S. pendulum* with other *Staurastrum* species, the disposition of the apical ornamentation clearly suggests an affinity with the *gracile - cingulum* group, though there is no indication of the ring of isthmal granules common to most members of this group. The possible relationship with *S. pingue* implied

by CROASDALE (1958, p. 32) is questioned, since there is a fundamental difference in the arrangement of the apical ornament in the latter and *S. pendulum*. However, *S. saltator* GRÖNBLAD, which NYGAARD (1949) suggests resembles *S. pendulum*, is clearly related to *S. pingue*, and it seems probable that in fact *S. pingue* may be synonomous with, or at least should renamed as a variety of *S. saltator*. Another species which may well be related to *S. pendulum* is *S. sublongipes* G. M. SMITH. In this, it is suggested that the apical ornament has become modified so that the central granule, of the three along each margin of the apex, appears as a verruca (cf. pl. 25 [1], fig. 18). The granules on either side of this are not shown in SMITH's original figures of this species (SMITH 1921, pl. XI, figs. 15 & 16), but in the quadriradiate form which GRÖNBLAD (1938, fig. 2 : 5c & d) has referred to this species, these granules on either side of the central verrucae are clearly visible. Whether his triradiate form (fig. 2 : 5 a) can properly be referred to the same taxa is doubtful, for in side view there is clearly an isthmal ornament of pairs of granules beneath each process, strongly suggestive of *S. pingue*.

It is of interest to note that the Scottish lochs in which *S. pendulum* var. *pinguiforme* has been found are ecologically very different from the comparatively shallow lake, Hostrup in mid-Jutland, from which the species was described. This Danish lake is stated by NYGAARD to be in the mixotrophic phase of eutrophy, with a Compound Phytoplankton Quotient varying between 3.3 — 6.4. The Scottish habitats are deep, oligotrophic lakes of glacial origin, having phytoplankton quotients of between 0.25 and 0.4, a pH range of 6.0 — 7.0 and alkalinities of between 2.6 and 8.0 p. p. m. $CaCO_3$.

S. MICRON WEST f. *MAJOR* f. nov., facies *QUADRATA*.

As already stated, owing to the inadequate original description of *S. paradoxum* and *S. gracile*, many radiate desmids have been referred to these two taxa. The illustration in RALFS monograph (1848) of *S. paradoxum* and a figure in the more recent monograph on British desmids (WEST and CARTER 1923, Pl. 145, fig. 1), also named as this species, represent it as a stout bodied, short-processed, quadriradiate form, quite different from the slender, typically planctonic forms described above. Similar robust forms have also been named as *S. gracile* (WEST and CARTER 1923, Pl. 144, fig. 3).

Dr. J. W. G. LUND of the Freshwater Biological Association has made rich gatherings on a number of occasions of a *Staurastrum* of this type (pl. 26 [2]—27 [3]) from a tarn at Tarn, near Silloth, Cumberland (personal communication). The taxonomy of the genus, however, is so con-

fused, that reference to the literature suggests that any of the following names might possibly be given to this *Staurastrum*.

S. paradoxum MEYEN
S. gracile RALFS
S. gracile var. *nanum* WEST
S. polymorphum var. *simplex* WEST & WEST
S. polymorphum var. *divergens* NYGAARD

The closest agreement, however, would seem to be with *S. polymorphum var. divergens* NYGAARD (1949) and especially with NYGAARD's Fig. 5, f, g, g_1 and h.

To appreciate fully the shape of this quadriradiate desmid, it must be viewed in side view in two positions: —

a) in its natural position of rest, with the 4 processes of each semicell diverging at angles of 45° from the plane of the microscope slide (pl. 26 [2], fig. 3 & 6).
b) in a less stable position, with one pair of processes parallel with the plane of the slide and the other pair at 90° to it (pl. 26 [2], fig. 1).

Viewed in position a), it will be seen that the semicell body is deeply cup-shaped, with a smooth outline and the semicell apex in this position can be seen to be convex or more frequently bi-undulate, each undulation bearing a small granule. In position b), the semicells appear broadly cyathiform and with a somewhat angular contour, due to the presence of a granule or small spine, on the semicell body above the isthmus. This granule or spine, would seem to be the last of a series of 4 occurring at intervals down the ventral side of each process and onto the body of the semicell (pl. 26 [2], fig. 1 & 5). This very distinctive cell shape, coupled with the four terminal spines on the short processes and the apical ornament of the semicells consisting of 4 intramarginal granules along each side (16 granules on each apex), points to the fact that this *Staurastrum* is closely related to *S. micron* WEST (see BROOK 1959 c, Fig. 2 D), and should be named *S. micron* f. *major* f. nov. fac. *quadrata*. „Differt a typo cellulis aliquandum spatiosis."

The reason for distinguishing these desmids from the species as forma *major* is that they are significantly larger than the maximum dimensions for this species quoted by WEST and CARTER (1923) and other authorities, and also than specimens described from the Jenner Herbarium in the British Museum, which had been incorrectly named on the mica as *S. paradoxum* (BROOK 1959 c). The sizes may be compared in the following table in which is also included the dimensions of *S. polymorphum* var. *divergens* NYGAARD, which is considered to be synonomous with it.

	S. micron West (1896)	S. micron Jenner Herb. (Brook 1959c)	S. polymorphum var. divergens (Nygaard 1949)	S. micron f. major fac. quadrata
L. sin. pro	8.5-11.5 μ	12.0-15.0 μ	22.5-28.0 μ	20.5-27.0 μ
L. cum. pro.	12.0-17.5 μ	20.0-22.0 μ	28.0-36.0 μ	25.0-31.0 μ
br. sin. pro.	7.0- 9.5 μ	8.0- 9.5 μ	— —	12.0-16.0 μ
br. cum. pro.	12.5-19.0 μ	20.0-23.0 μ	25.0-38.0 μ	25.0-32.0 μ
br. isthm.	3.0- 3.5 μ	5.5- 6.5 μ	7.0- 8.5 μ	7.5- 8.5 μ

S. MICRON var. *PERPENDICULATUM* (GRÖNBLAD) nov. comb.

GRÖNBLAD (1948) has already cast doubt on the identity of *S. iotanum* WOLLE, another of the *Staurastrum* species inadequately described and figured originally, so that as GRÖNBLAD states, it can equally well include *S. tetracerum* (f. 3-*radiata*), *S. micron*, *S. pseudotetracerum*, or *S. paradoxum* var. *parvum*. It is very apparent that GRÖNBLAD's var. *perpendiculatum* of *S. iotanum* GRÖNBLAD (1920, Tab. III, fig. 72—73) is closely related to *S. micron* by virtue of its size, and especially by the conspicuous emarginate spines seen on the lateral margins of the semicells. This desmid, previously unrecorded from the British Isles has recently been found in plankton from L. Bofin, Ireland (ROUND and BROOK 1959a) (pl. 27 [3], fig. 4 & 5). In view of its unmistakeable affinity with *S. micron* (pl. 27 [3]), fig. 6), and the very doubtful status of *S. iotanum*, it is proposed to rename it *S. micron* var. *perpendiculatum* (GRÖNBLAD) nov. comb. Other species which may well belong to the *S. micron* group and should be reinvestigated, are *S. chavesii* BOHLIN, *S. heimerlianum* LÜTKEMÜLLER and *S. vestitum* var. *parvum* NYGAARD.

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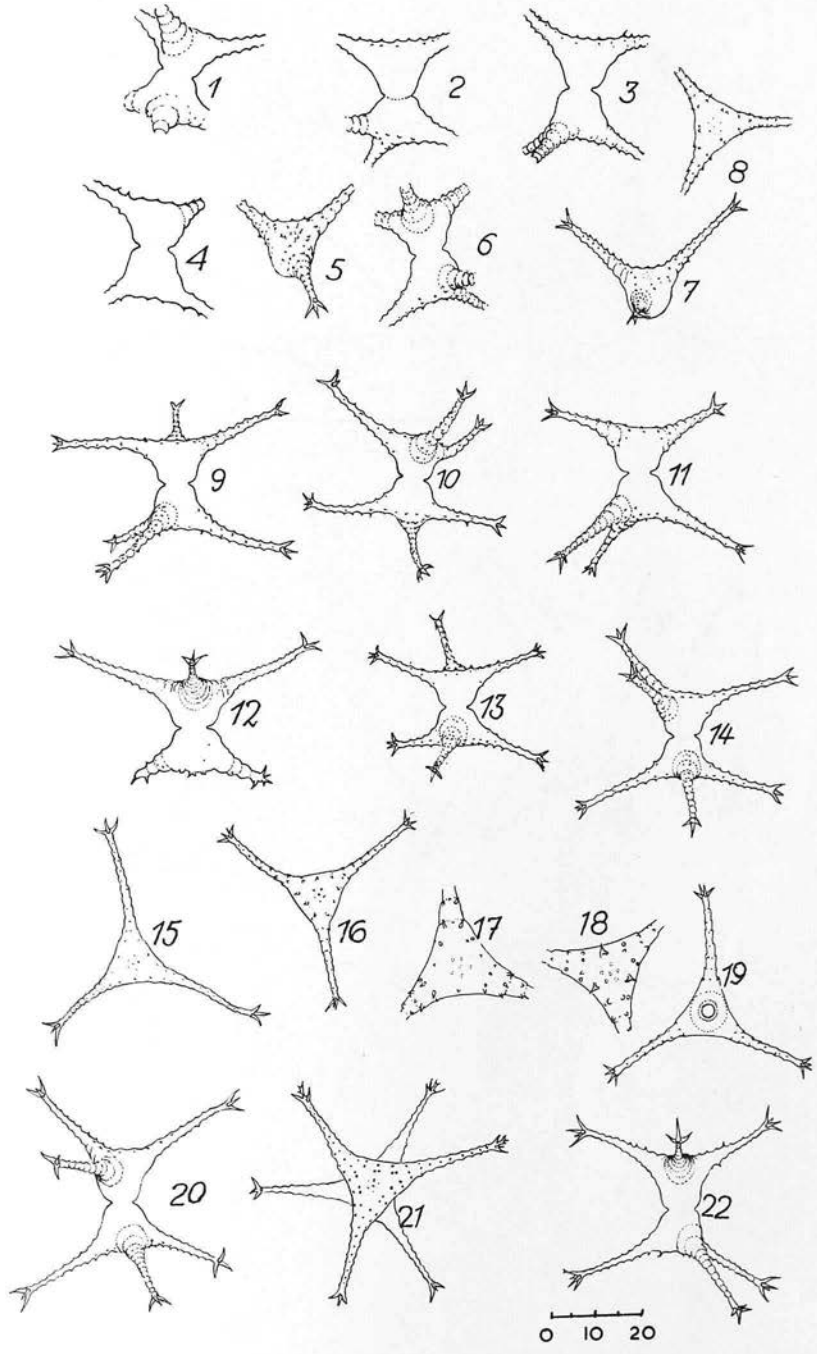
EXPLANATION OF THE PLATES

Plate 25 (1), fig. 1—8: *S. pendulum* var. *pinguiforme* CROASDALE from Loch Rannoch, Perthshire.
1. — 4 & 6 side views showing shape of semicells.
5 & 7 oblique views showing apical ornament and mucilage pores in central area.
8. apical view.
S. pendulum var. *pinguiforme* CROASDALE
Fig. 9—22.
1, 2, 3 & 5 side views of specimens from Loch Ericht, Perthshire.
4. side view of aberrant speciment from Loch Rannoch.
6, 12 & 14. side views of specimens from Loch Tummel.
7—10 & 13. apical views showing variation in ornamentation.
11. isthmal view.

Plate 26 (2): *S. micron* f. *major* f. nov. fac. *quadrata* from Tarn tarn, Cumberland.
1. Side view in position 'b' (see text).
3 & 6. Side views in position 'a'.
2 & 4. apical views showing ornamentation.
5. isthmal view.

Plate 27 (3): 1—3. *S. micron* f. *major* fac. *quadrata* from Tarn tarn, Cumberland.
4 & 5. *S. micron* var. *perpendiculatum* nov. comb. from Lough Bofin, Ireland.
6. *S. micron* West from Loch Mhor, Inverness.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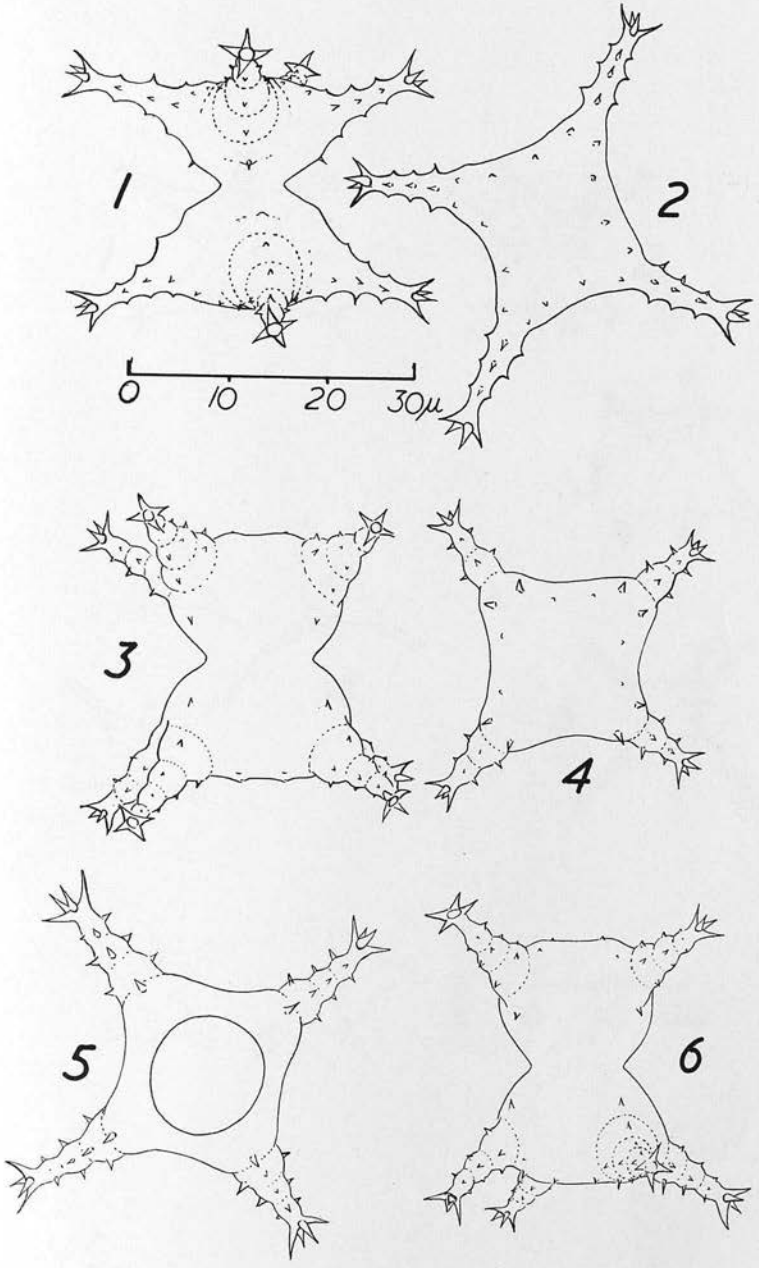

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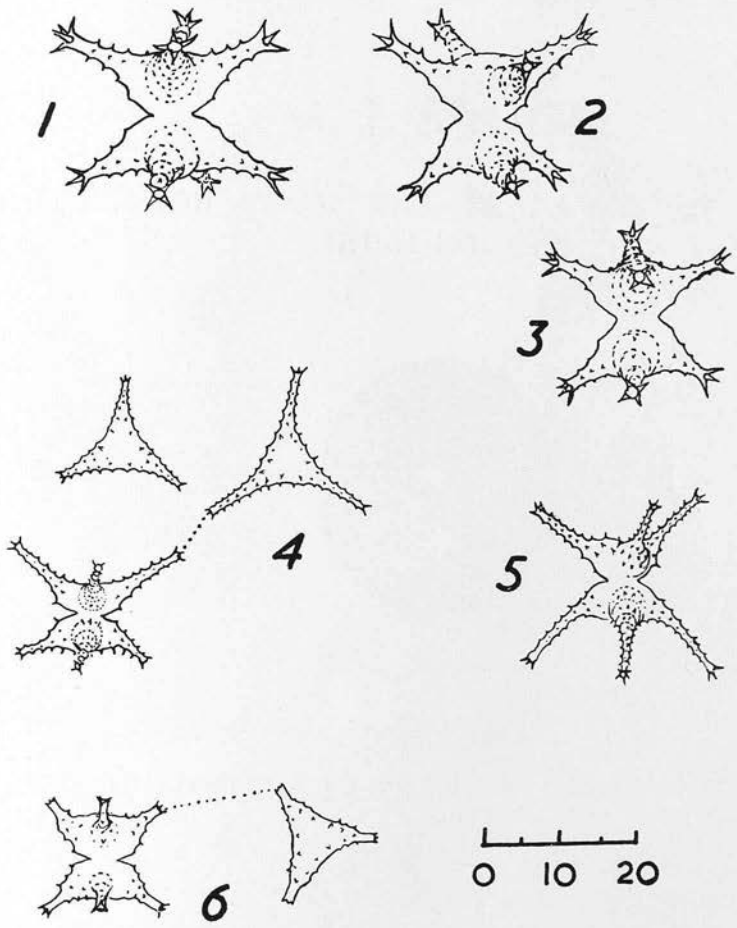

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A. J. BROOK

DESMIDS FROM THE PLANKTON OF SOME IRISH LOUGHS

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6.

DESMIDS FROM THE PLANKTON OF SOME IRISH LOUGHS

By A. J. BROOK

(Freshwater Fisheries Laboratory, Pitlochry, Scotland)

[Read 24 June, 1957. Published 10 February, 1958]

INTRODUCTION

Dr. F. E. Round, of the University of Bristol, has kindly put at my disposal a considerable number of plankton samples collected from freshwater loughs in various parts of Ireland, many of which are rich in desmids, especially of the genus *Staurastrum*. The present paper deals only with the morphology of the more interesting and unusual desmids observed in these collections, some of which are new to the British Isles, some hitherto unrecorded from Ireland, while others show small, but distinctive differences from specimens previously described in the literature and thus are worthy of being placed on record. Although twenty-six loughs in all were sampled, desmids from only the following are mentioned in this paper:—Lough Erne, L. Melvin, L. Key, L. Corrib, L. Beltra, L. Conn and L. Cullin (Co. Mayo), Kylemore Lough and Levally Lough (Co. Galway), Gara Lough (Co. Sligo) and Loughs Oorid, Ardderry, Aunierin and Bofin (all beside the Galway-Clifden road, near Maam Cross). A joint paper is, however, in preparation on the distribution of all groups of plankton algae from all the loughs sampled and on the probable trophic status of their waters as shown by their algal floras.

Dr. Round has asked me to express his thanks to Professor D. A. Webb of Trinity College, Dublin, who afforded much valuable assistance in the sampling of many of the loughs.

Micrasterias conferta Lund

A small form of this, the rarest of the British *Micrasterias* species, which has previously been found in the British Isles only in parts of Scotland, was found in the plankton of Lough Bofin. The specimen illustrated here (fig. 1) approaches the var. *hamata* Wolle in the somewhat uncinate form of the lateral angles of the polar lobes (cf. West and West, 1905, Pl. 43, fig. 9), the overlapping of the basal lobules in adjoining semicells being very marked. Cells 70–75 μ l., 71–75 μ brd, 15 μ brd at the isthmus.

Cosmarium alpestre Roy and Biss

Occasional specimens of this montane species, which has not been previously found in Ireland, were present in the plankton of Lough Bofin and L. Aunierin. The cells were of somewhat smaller dimensions than the specimens described by Roy and Bissett (1894), though having the same general proportions, being 68–70 μ l. and 56–59 μ brd, with a slight isthmal constriction, the cells in this region measuring 54–55 μ in breadth. The row of larger punctae which borders each side of the broad isthmus was quite distinct in all specimens.

C. pseudoprotuberans Kirch

All the specimens examined were small, their dimensions falling within the lower end of the size range for this species, being from 20–23 μ l. and 18–20 μ brd, and 8 μ brd at the isthmus. In some of the specimens from Lough Corrib, fine strands of mucilage were seen to be extruded from the delicate mucilage pores which cover the cell wall (fig. 2). This desmid, which has not been recorded from Ireland, was rare in Lough Aunierin and L. Corrib.

C. quinarium Lund

Specimens larger than those previously recorded in Britain have been found in Lough Bofin, being 48–52 μ l. and 39–47 μ brd, and 11–12 μ at the isthmus. The series of 10 rounded granules just within the outer margin of each semicell was very distinct in all specimens, though the central granules, arranged in two transverse rows, were less prominent and did not always, as stated by West and West (1908, p. 216), consist of 3 in the upper and 2 in the lower series. In some specimens the upper row contained 5 and the lower 4 granules (fig. 3).

C. entochondrum West and West

Occasional specimens of this species, previously recorded from only one locality in Sutherland, Scotland (West and West, 1908, p. 193, Pl. 87, fig. 17), have been found in Lough Bofin (fig. 4). They were of somewhat larger dimensions than those given by the Wests, being 48 μ l. and 45 μ brd, and 12·5 μ at the isthmus. The very characteristic granules, one large one on each side of the isthmus, one on each side of the apex and one at each basal angle of the semicell, were present in all specimens. Immediately within the apex and apical angles there is an arc-like series of granules, 6 in number according to the Wests, but which in the Irish material most frequently numbered 8. Below this arc, across the centre of each semicell, was a row of 3 to 5 smaller granules.

C. contractum var. *gartanense* West and West

Some slightly shorter though broader specimens of this variety (60 μ l., 43–45 μ brd, isthmus 10 μ brd) with typically retuse apices to their semicells were found to be quite frequent in the plankton of Lough Bofin (fig. 5). Several specimens were distinctive in the possession of marked thickenings on the cell wall in the region of the isthmus (cf. Taylor, 1933, Pl. 50, fig. 5).

Xanthidium antilopeum var. *hebridarum* West and West forma

Reference to the Wests' illustrations of *Xanthidium subhastiferum* West (West and West, 1911, Pl. 106, especially figs. 7 and 9) would suggest that the specimen illustrated in fig. 6, which is from Lough Bofin, should be referred to this species. However, the distinctive scrobulations on the central area of each semicell would seem to be a contrary character. The slightly angular shape of the apex of each semicell on the other hand indicates, it is believed, the positions which might be occupied by spines, but which in this specimen are completely suppressed. Thus if fig. 6 is compared with Pl. 110, fig. 1, in West and West (1911), it becomes clear that the specimen in question is a reduced form of *X. antilopeum* var. *hebridarum* lacking apical spines in each semicell. Dimensions of cell body without spines; 65 μ l., 57 μ brd, 18 μ brd at the isthmus.

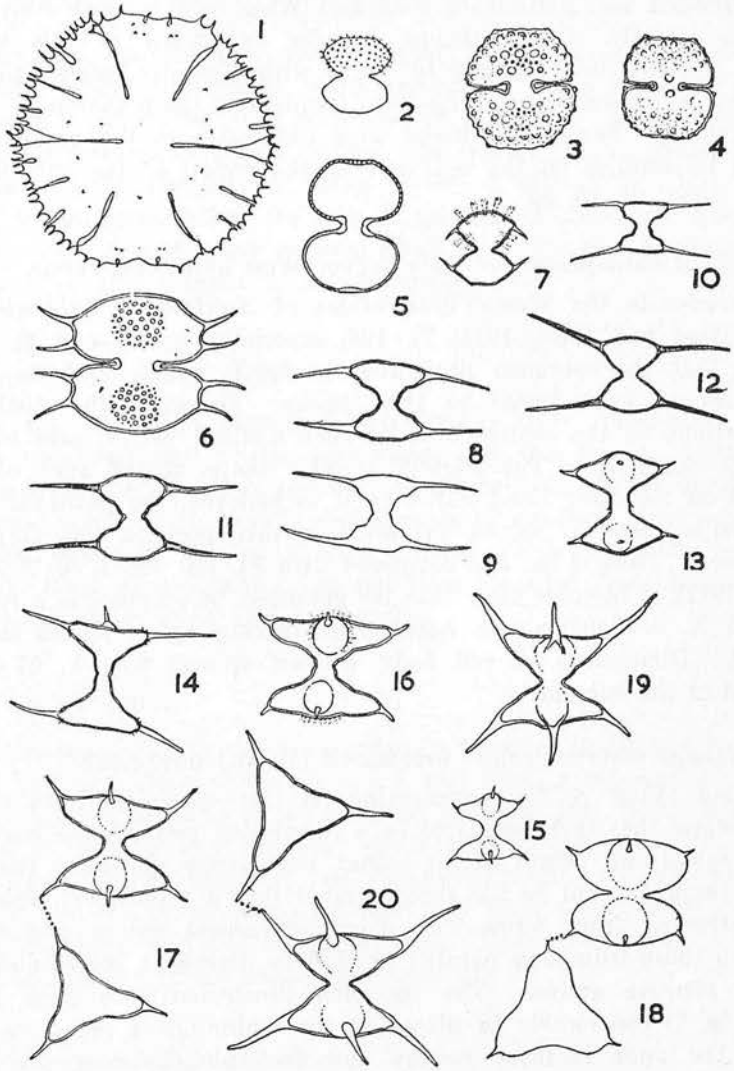
Staurodesmus glabrus facies[1] *brebissonii* (Racib.) nov. comb.

Teiling (1948, p. 70), commenting on this species and its various forms, states that there seems to be a correlation between the curvature of the apices and length of the spines, the shorter the latter the more convex the apex, and he has demonstrated that a typological series can be constructed from forms with short convergent spines and convex apices to those with long parallel or slightly divergent spines and even slightly concave apices. The specimen illustrated here from Lough Bofin (fig. 7) can clearly be placed at the beginning of this series, and indeed the apex is more convex and the spines shorter and more convergent than any of the specimens figured in Teiling's paper, or the type illustrations (Messikommer, 1942, Taf. XI, fig. 5, and Smith, 1924, Pl. 85, fig. 9).

S. joshuae (Gutw.) Teiling

This desmid, which because of its distinctive character Teiling (1948) has elevated to specific rank, does not appear to have been recorded from Britain, even by one of its several synonyms. I have, however, found it in a considerable number of lakes in various parts of Britain, while in these Irish samples it is abundant in Lough Aunierin. It can be confused

[1] See Teiling, 1950, pp. 324–326.



1. *Micrasterias conferta* Lund.
2. *Cosmarium pseudoprotuberans* Kirch.
3. *C. quinarium* Lund.
4. *C. entochondrum* West and West
5. *C. contractum* var. *gartanense* West and West
6. *Xanthidium antilopeum* var. *hebridarum* West and West forma
7. *Staurodesmus glabrus* fac. *brebissonii* (Racib.) nov. comb.

8–10. *S. joshuae* (Gutw.) Teiling

11. *S. subtriangularis* (Borge) Teiling
12. *S. subtriangularis* var. *inflatus* (West and West) Teiling
13. *S. cuspidatus* (Bréb.) Teiling

14–16. *S. cuspidatus* var. *canadense* (G. M. Smith) nov. comb.

17. *S. dejectum* (Bréb.) Teiling
18. *S. dejectum* var. *inflatum* (West) Teiling

19–20. *S. curvatus* var. *inflatus* (Lind and Pearsall) nov. comb.

with *Staurodesmus subtriangularis* (Borge) Teiling (see below), though it is much more angular than the latter, with a longer and more slender isthmus which in most British specimens show a marked indentation at the sinus (cf. Teiling, 1948, p. 67 and fig. 3). The spines may be convergent (fig. 8), but more generally they are parallel to slightly divergent in their disposition. In contrast to *S. subtriangularis* the spines are solid but more delicate, while the semicell apices are flatter (figs. 9–10).

S. subtriangularis (Borge) Teiling

A drawing of a typical specimen of this desmid, which may be confused with the above mentioned species, is shown in fig. 11. It can be seen that the semicells in this are more rounded and robust than in *S. joshuae* and have distinctly convex apices, while the cell wall at the sinus is slightly thickened and the spines are usually hollow. This species was found in Lough Bofin, Ballynahinch Lough and L. Oorid.

The variety *inflatus* (West and West) Teiling of this species also occurs in Lough Aunierin (fig. 12).

S. cuspidatus (Bréb.) Teiling

Teiling (1948, p. 60) remarks that this species appears in a considerable number of forms connecting the allied species *curvatus, aristiferus* and *apicuatus,* a remark which rather suggests that it has in fact become one of the "rubbish-heap" taxa (see Grönblad, 1948, p. 420) into which many forms of monospinous desmids with elongated isthmuses have been thrown. The specimen from Ballynahinch Lough (fig. 13) is tentatively referred to this species though it is conceded that it may well be a form of *S. curvatus* var. *elongatus* (G. M. Smith) nov. comb. (see below). Fig. 13 should be compared with figs. 25–26.

S. cuspidatus var. *canadense* (G. M. Smith) nov. comb.

In contrast to the species, this variety seems to be much more clearly defined, the slender, elongated isthmus having a very distinctive constriction where the two semicells join. The semicells are broader than in the type, the angles tapering gradually at first and then suddenly more prominently towards their extremities which are tipped with long, straight, or gently curving and slightly divergent spines. Around the more acutely tapering region of the angles there is a double ring of mucilage pores, often having a small plug of mucilage extruded from them and which show up distinctly, even without staining (fig. 14) (cf. *Staurastrum cuspidatum* var. *coronulatum* Gutw.). This desmid was rare in Kylemore and Ballynahinch Loughs.

A small form of *Staurodesmus* of similar dimensions and apparently identical in all but the length of the spines with the specimen figured by Taylor (1934, Pl. 33, fig. 5) from Newfoundland, and which he has

referred to this variety *canadense* occurred in Lough Bofin (fig. 15). No mucilage pores were, however, observed around the angles of these small forms.

Frequent in Lough Bofin, L. Oorid and L. Ardderry was a larger form of *Staurodesmus* with short spines, but again with a slightly elongated isthmus and having a very distinct constriction where the two semicells join (figs. 16–17). Thus these forms may also be referred to the var. *canadense*. However, the typical mucilage pores round the angles were absent, though other pores with extruded mucilage were very apparent on many specimens. These extend over the apex of each semicell and downwards on to the sides between the angles of the semicells. This arrangement of mucilage pores should be compared with that observed in the forms of *S. curvatus* var. *inflatus* (Lind and Pearsall) nov. comb. described below (see also figs. 22–23).

S. dejectum (Bréb.) Teiling

Both Grönblad (1948) and Teiling (1954) have commented on the considerable confusion about the limits of this species which the former (p. 420) regards as one of "those rubbish-heaps, of which there are unfortunately so many in desmid taxonomy". Both of these authorities urge that Ralfs' figure of the species from his British Desmids (1848), Pl. XX, fig. 5*a*, but not 5*b*, *c* or *d* (also labelled *S. dejectum*), should be taken as the typical form. Those in Pl. 129, figs. 9–12 of West and Carter's monograph (1923) are also quite erroneous. Teiling gives the following characters as important; "hemisomate court et semicirculaire à apex aplati avec à chaque angle, une épine verticale courte; le sinus est arrondi". He emphasises, however, that of these the most important character is the rounded sinus, with the isthmus sometimes slightly elongated. Moreover, he believes that the shape of the apex and the length and direction of the spines are less constant characters and thus of less taxonomic value. Because of the shape of its sinus, only the desmid shown in fig. 17 from Lough Bofin can be referred to this species. The var. *inflatum* (West) Teiling (fig. 18) has been found in Lough Melvin.

S. curvatus var. *inflatus* (Lind and Pearsall) nov. comb.

Some very robust specimens of this desmid characterised by their slightly convex dorsal and ventral walls when observed in side view, and also by their very strongly developed diverging spines, have been found in Lough Beltra and L. Ballynahinch (figs. 19–20). These forms show quite a strong resemblance to *S. dejectum* (cf. fig. 18), but are distinguished by their much more acute sinus. Smaller forms with shorter and more slender spines and less angular sinuses, which would seem to be intermediate between this variety and *S. dejectum* occur in Lough Bofin and Ballynahinch Lough (figs. 22–23). The mucilage pores on many of these specimens, which extend over the centre of the apex of

each semicell and downwards on to the sides between the angles of the semicells, were very conspicuous.

Another smaller form with a markedly convex apex and less divergent spines, but with the same arrangement of mucilage pores as the forms described above, also occurs in Ballynahinch Lough (fig. 24). This should be compared with the drawing of *S. megacanthus* (Lund.) nov. comb. (= *Staurastrum megacanthum* Lund.) in West and Carter (1923, Pl. 131, figs. 7–8).

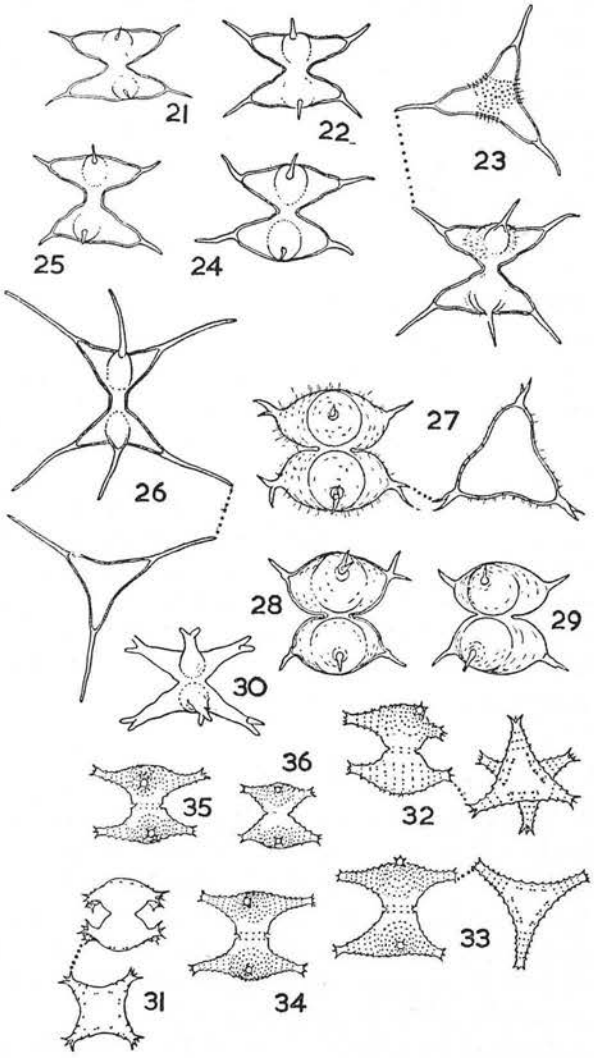
S. curvatus var. *elongatus* (G. M. Smith) nov. comb.

Two distinct forms which can be referred to this variety have been observed in the present samples. One which seems closely allied to the desmid shown in fig. 22 and named *S. curvatus* var. *inflatus*, differs only in the possession of an elongated isthmus (fig. 25). Because of this latter character and the angularity of the semicell angles, these forms could possibly be referred to *S. cuspidatus* (cf. fig. 13 and Nygaard's *S. cuspidatum* var. *acuminatum* in Nygaard, 1949, p. 89, fig. 44). The other (fig. 26) is a more slender form, differing from the forms of this variety figured from the Irish plankton by Lind and Pearsall (1945, figs. 9 and 11), in possessing distinctly concave semicell apices, slightly convex ventral walls and much more slender spines. This form was quite frequent in Lough Oorid and L. Ardderry.

Staurastrum pelagicum West and West

Specimens of this species have been found in the plankton of Lough Corrib, the locality from which it was originally described in 1902. All the specimens observed in the present collection, however, were much more tumid than those figured by the Wests, the sinus being distinctly closed and the semicell apices markedly convex (figs. 27–29). In fact some specimens were initially mistaken for *Staurodesmus dejectum* var. *inflatum* (see fig. 18), especially when in certain cases some or all the angles were tipped with a single solid spine, instead of the bifurcate spine which is said to be typical. Added to this, in none of the specimens were the four well-separated series of granules which encircle the angles of the semicells at all distinctive, though the minute pores which cover the cell walls were often seen to have delicate strands of mucilage extruded from them (fig. 27).

In West and Carter (p. 125) it is stated that this species is perhaps most closely related to *Staurastrum avicula* Bréb. My own observations on this latter species and its possible relationships (Brook, 1957) do not support this view, any similarities between the two being very superficial. If comparisons are to be drawn at all, *S. pelagicum* surely resembles more closely *S. subcruciatum* Cooke and Wills, especially in the form of its processes and spines (see also Taylor, 1934, p. 196).



21–24. *Staurodesmus curvatus* var. *inflatus* (Lind and Pearsall) nov. comb.
25–26. *S. curvatus* var. *elongatus* (G. M. Smith) nov. comb.
27–29. *Staurastrum pelagicum* West and West
30. *S. brachiatum* Ralfs
31. *S. ornatum* Turn.
32. *S. proboscidium* (Bréb.) Arch.
33–36. *S. borcale* West

S. brachiatum Ralfs

Occasional specimens, proportionately shorter and with less divergent processes than those depicted in West and Carter (1923, Pl. 142, figs. 1–7), were present in Lough Bofin (fig. 30).

S. ornatum Turn

A quadriradiate form of this small desmid occurs in Lough Bofin. In this, the apices of the semicells are very convex and the short processes markedly convergent. The sides of the body are without ornament, but the apical ornament of intramarginal granules or verrucae is very distinctive. Fig. 31, depicting this species, should be compared with Grönblad's illustrations of specimens from Tvärminne, Finland (Grönblad, 1934, fig. 4, 39–40). It should also be compared with some of the forms of Nygaard's *S. polymorphum* var. *divergens* (Nygaard, 1949, especially fig. 54*a, f* and *g*), which differs only in the possession of strongly divergent processes.

S. proboscidium (Bréb.) Arch.

Small forms of this species, which in the development of their processes approach the var. *productum* of Messikommer (1942, Pl. 17, fig. 3), have been found in small numbers in Lough Bofin. In side view the plant illustrated here (fig. 32) has quite a strong resemblance to Ralfs' illustration of the species (Ralfs, 1848, Tab. XXIII, fig. 12*b* and *c*). In some of the specimens the isthmal ring of granules was very indistinct. Cells 25–30 μ l., 30–33 μ brd with processes; 8 μ brd at the isthmus.

S. boreale West

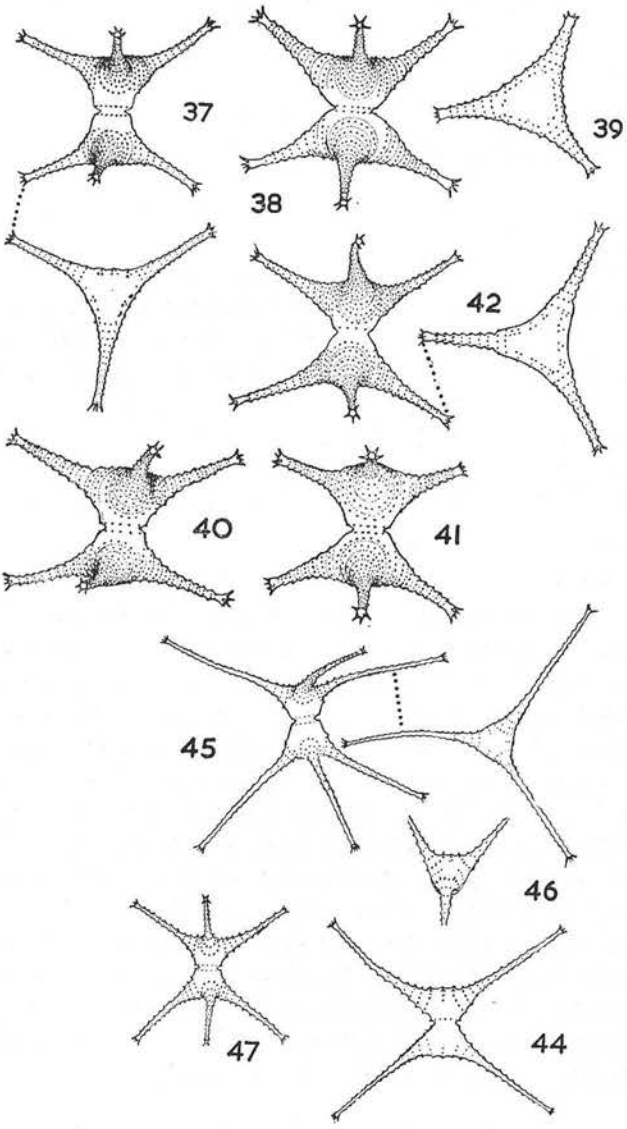
Few of the figures published of this desmid since the original illustrations of the Wests (West and West, 1905, Pl. 146, fig. 25) seem to agree convincingly with the latter, most being more robust, with shorter processes and which thus would seem to have closer affinities with *S. proboscideum*. The plants from Lough Bofin which can be referred to this species, however, agree in all respects with the Wests' description and figures, especially in the cup-shaped form of the semicells and the comparatively long and slender processes which are nearly horizontal, or only slightly divergent in their disposition (figs. 33–35). The small form (fig. 36) in which the rings of granules round the semicell body just above the isthmus could not be discerned must also be referred to this species, though forms like this would by some authorities be referred to the doubtful species, *S. polymorphum* Bréb. Cells 26–29 μ l., 33–36 μ brd with processes, 7 μ brd at the isthmus.

This desmid does not seem to have been previously recorded from Ireland.

S. cingulum (West and West) G.M. Smith

Clearly related to the foregoing species are the typical slender bodied forms of *S. cingulum*, though differing most markedly in the possession of long, narrow divergent processes (fig. 37). This species which has

previously only been recorded in Ireland (as *S. paradoxum* var. *cingulum*) from Lough Currane has now been found in Ballynahinch and Kylemore Loughs.



37. *S. cingulum* (West and West) G. M. Smith
38–39. *S. cingulum* var. *obesum* G. M. Smith
40–42. *S. cingulum* forms
44–47. *S. chaetoceras* (Schröder) G. M. Smith (46 is an oblique view of the semicell apex of a triradiate form of this desmid.)

S. cingulum var. *obesum* G. M. Smith

This variety, which has not previously been recorded from the British Isles, occurs in Lough Beltra (fig. 38), while forms intermediate in character between this variety and the type species have been observed in the samples from L. Key, Gara Lough and L. Corrib (figs. 39–42).

S. chaetoceras (Schröder) G. M. Smith

Another species of planktonic *Staurastrum* previously unrecorded from the British Isles and which like *S. cingulum* possesses an isthmal ring of granules, but which in all other respects is quite distinctive, is *S. chaetoceras*. It occurs quite frequently in the eutrophic Lough Erne and, as seems to be the rule with this species (see Smith, 1924, p. 99), both bi- and triradiate forms were present in the sample (figs. 43–47). The processes of these plants were more slender than normal, tapering in some cases to 2 μ in breadth at their narrowest part, while their length varied considerably between specimens, ranging from 15 to 50 μ.

S. longipes (West and West) Teiling

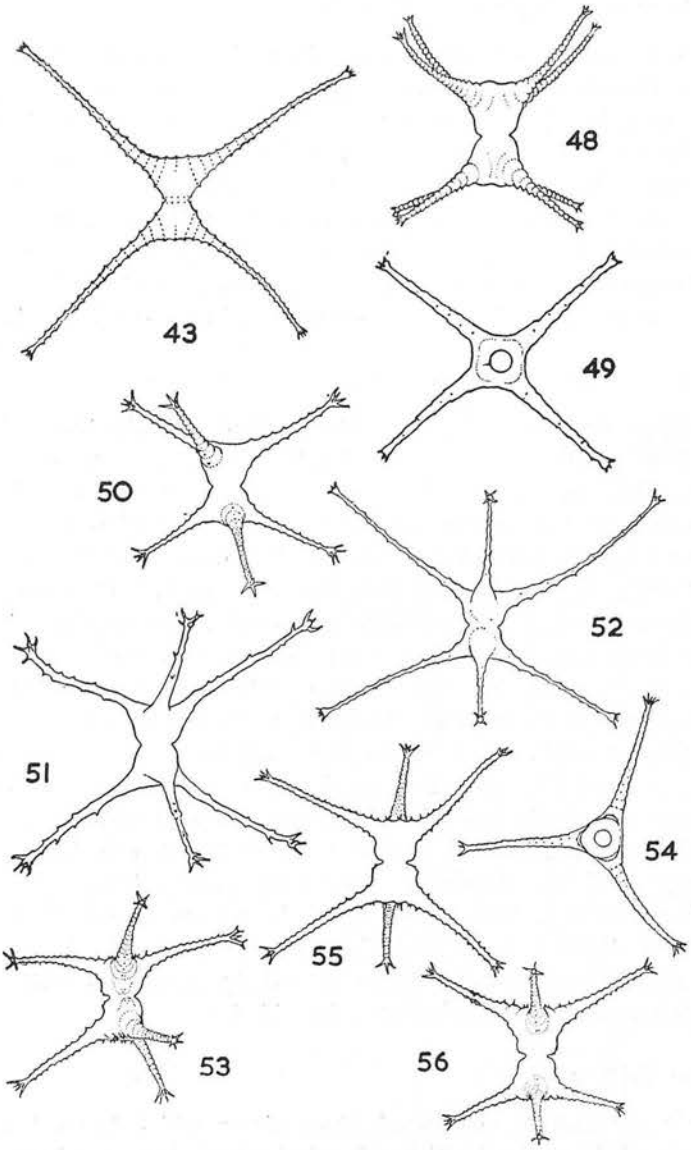
This appears to be one of the most abundant and widespread *Staurastra* in the Irish plankton (West and Carter, 1923, p. 104, and Lind and Pearsall, 1945, p. 317). However, several quite distinct forms have been recognised during the present investigation which do not seem to have been recorded previously. The most frequent was that occurring in Lough Corrib, L. Melvin and Ballynahinch Lough. This was a robust. quadriradiate form with gracefully upcurved processes (figs. 48–49) and differing from the more typical form (fig. 50, and West and Carter, Pl. 146, figs. 2–3) in that the apex instead of being flat or slightly concave, is biundulate; the sinus when viewed from certain aspects appears much deeper than normal owing to the fact that the body of the semicell is distinctly rectangular in section as shown by the dotted line in fig. 49.

A form with quite typical body shape but with aberrantly decorated processes has been observed in Ballynahinch Lough (fig. 51). Also from this lough and L. Aunierin, specimens approaching Teiling's var. *contractum* (Teiling, 1946, p. 81, fig. 5) have been found, those from the latter being distinctive in that they possess unusually long and very slender processes (fig. 52). These should be compared with the very slender processes of *S. chaetoceras* (figs. 44–47).

S. pingue Teiling

This is yet another species of *Staurastrum* which has not previously been recorded from the British Isles, but which has now been found in the Irish plankton from Kylemore and Ballynahinch Loughs and L. Beltra (figs. 53–57). It also is quite common at times in the plankton of several

English and Scottish lakes. The main characteristics of the Irish plants agree well with Teiling's original description (Teiling, 1942), though many tend to approach *S. leutkemuelleri* Donat, in that on each of the angles of the semicell body just above the isthmus, three granules can be clearly discerned. These are noticeable in the specimens from Ballynahinch Lough and especially in the robust form found in Levally Lough (fig. 58).



43. *S. chaetoceras* (Schröder) G. M. Smith
48–51. *S. longipes* (West and West) Teiling
52. *S. longipes* var. *contractum* Teiling
53–56. *S. pingue* Teiling

S. arachne Ralfs, forma

Occasional specimens of this desmid whose form and dimensions correspond much more closely with those described and figured by Smith from plankton samples collected from the Capel Curig lakes in Wales by W. and G. S. West (Smith, 1924, p. 111, fig. 13), than those in West and Carter (1923, Pl. 150, fig. 1), have been observed in the material from Lough Bofin. The slightly oblique top and bottom views of a semicell from this lough show, in top view (fig. 59 A), the apex ornamented by 5 strong verrucae, one between each of the five processes. The bottom view of the semicell (fig. 59 B) shows the side of the body, normally quite smooth, decorated by 5 rounded granules, one between each process, a feature hitherto undescribed for this species.

S. inflexum Bréb.

A few individuals of this species with very slender cup-shaped semicells, thus differing quite radically from forms of this species previously described from Britain, have been found in Lough Bofin (fig. 60). These specimens, especially with regard to the cup-shaped form of the semicells would seem to be more akin to the form of this desmid described by Taylor (1934, Pl. 35, fig. 16), from Newfoundland. It should also be compared with the form of *S. incurvatum* West and West figured by Grönblad from Finland (1938, fig. 1 : 12).

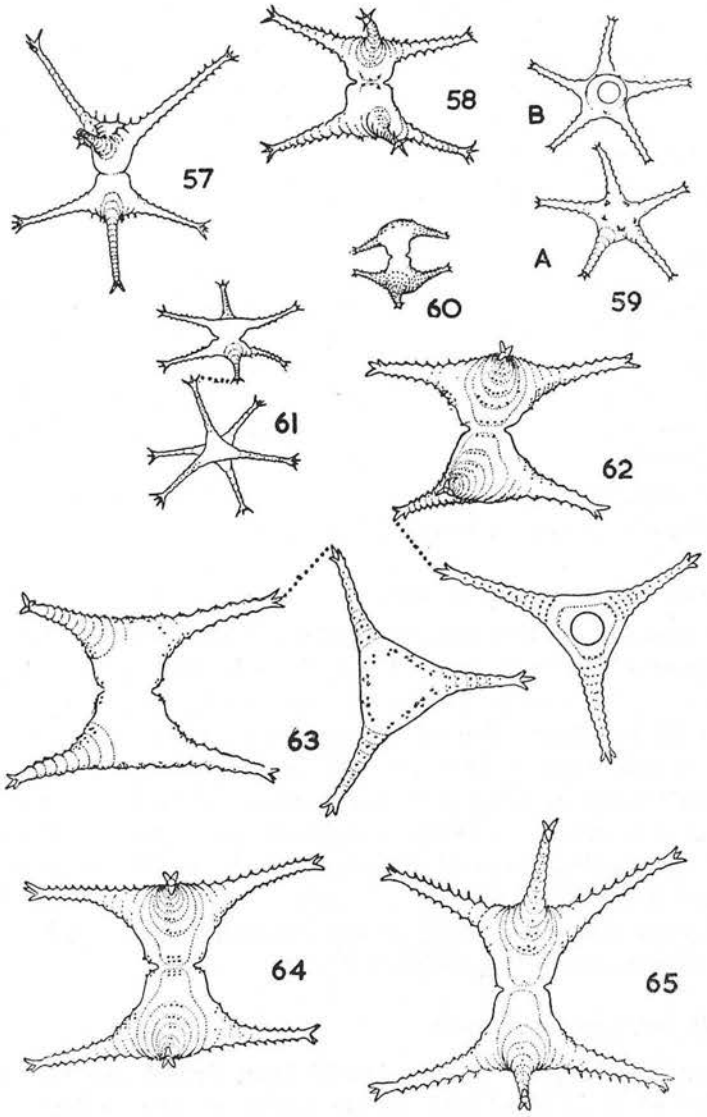
S. subgracillimum West and West

Some specimens of this rare *Staurastrum,* hitherto recorded in Britain from only one locality in Ireland and three in Western Scotland, have been seen in the sample from Lough Bofin (fig. 61). They agree in general with the description of this species in West and Carter (1923, p. 118), though differ in that the processes in side view show a slight divergence instead of being horizontal. Also their apical spines, always said to be very minute in British specimens, are clearly much more like those of the American form of this species (West and West, 1896, p. 263, Pl. 17, figs. 3–4), being comparatively large and spreading. All the cells observed were typically twisted at the isthmus. Cells 10 μ l., 12 μ brd breadth with processes 40 μ, isthmus 5 μ brd.

S. sebaldi var. *ornatum* Nordst

Neither West's figure of this desmid from British material, nor the description of it in West and Carter (1923, p. 168) indicate that the semicells may on occasions bear granulae on the body in the region of the isthmus. However, all specimens of this variety from the Irish plankton seem to be ornamented in this way, though in this connection it is important to point out that Teiling, in his detailed study of the *manfeldtii-sebaldi* group of *Staurastrum* species (Teiling, 1947), indicates

that the desmid which in West and Carter (Pl. 148, fig. 2) had been named *S. manfeldtii* and which does bear a distinct isthmal decoration, can be taken as the type for *S. sebaldi* var. *ornatum*. Thus the specimens figured here from Lough Corrib and Ballynahinch Lough (figs. 62–63) would also seem to be quite typical.



57–58. *S. pingue* Teiling
59. *S. arachne* Ralfs. forma
60. *S. inflexum* Bréb.
61. *S. subgracillimum* West and West
62–63. *S. sebaldi* var. *ornatum* Nordst
64–65. *S. sebaldi* var. *ornatum* fa. *planctonicum* Teiling

A series linking the var. *ornatum* with the fa *planctonicum* Teiling. can be built up from the forms present in the Irish plankton, and especially significant in this connection are several dichotypical specimens which have been observed in some of the loughs (figs. 64–66). This series shows a gradual elongation and alteration in semicell shape from cup-shaped to subcylindrical, coupled with a tendency to increasingly divergent processes and a reduction in the prominence of the granules ornamenting the isthmal region of the body. Indeed the almost total absence of isthmal and sub-brachial ornament, and the very prominent dorsal spines on the processes, suggests that some of the specimens occurring in Lough Erne and L. Arrow (see lower semicells in figs. 65 and 66), may in fact be referred to *S. planctonicum* Teiling. The shape of the lower semicell of the Lough Arrow specimen (fig. 66) is, moreover, suggestive of the var. *bulbosum* of this species.

Another form closely allied, if not identical to this latter variety, especially in the annular inflation of the slender semicell body above the sinus is shown in fig. 67. This desmid seems to be identical with *S. gracile* var. *cyathiforme* West and West, which Teiling (1947) has suggested is also derived from *S. sebaldi*. The principal differences between the desmid figured here and in West and Carter (1923, Pl. 144, fig. 12) from Teiling's var. *bulbosum* would seem to be in the dorsal ornamentation of the processes, the prominent dorsal spines being absent in the former. The general pattern of the apical ornament, however, is identical with that found on other members of the *manfeldtii-sebaldi* group (see also Nygaard, 1949, fig. 56), while a most important common character is the enlargement and forward direction of the ventral spine of the three which tip the processes of all members of this species group.

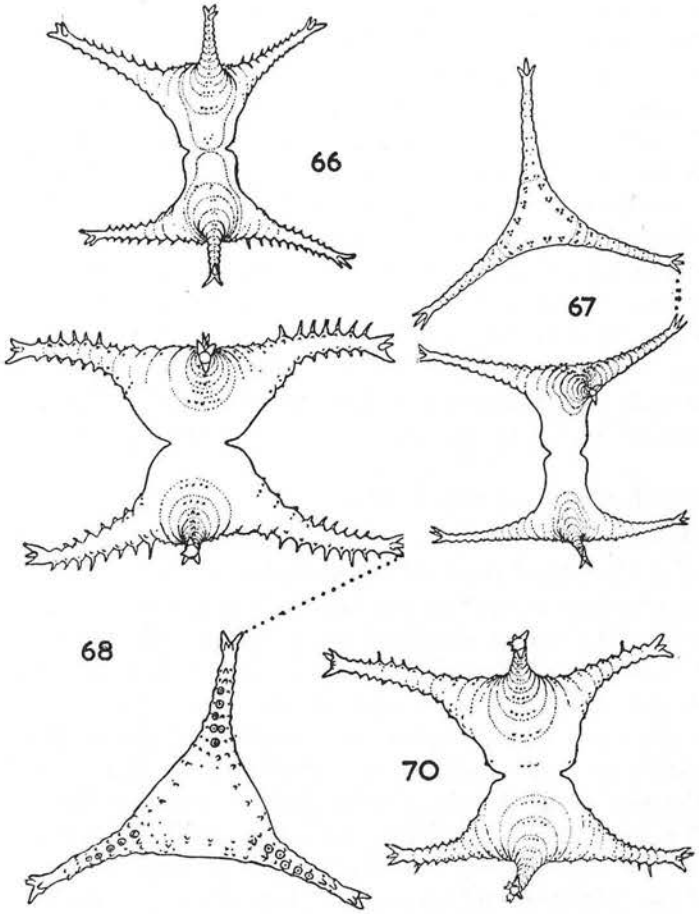
S. dorsidentiferum West and West

As originally described (West and West, 1906, p. 103) this desmid is said to be distinguished from all other species by its large cells which are free from ornament except for the row of stout spines on the top of each process (fig. 68). Lough Corrib, from which the present material was collected, was one of the first localities from which this species was described, and indeed this species has not yet been found outside Ireland. The present specimens conform to the original description in such characteristics as size, shape of the semicells, disposition of the processes and in the row of stout spines which are borne along the top of each. They differ, however, in that the semicells bear considerable ornamentation in addition to the characteristic dorsal rows of large spines, the apices having four intramarginal granules lying equally spaced in an arc between each process, while external to these there may be one or two smaller granules. The dorsal and ventral sides of the processes each bear a series of granules in lateral rows of from 2–5, depending on their position on the processes. One of the granules in each of these rows,

usually the middle one, is greatly enlarged especially on the dorsal side. It is these which form the characteristic row of stout spines mentioned above and which are the outstanding feature of this species.

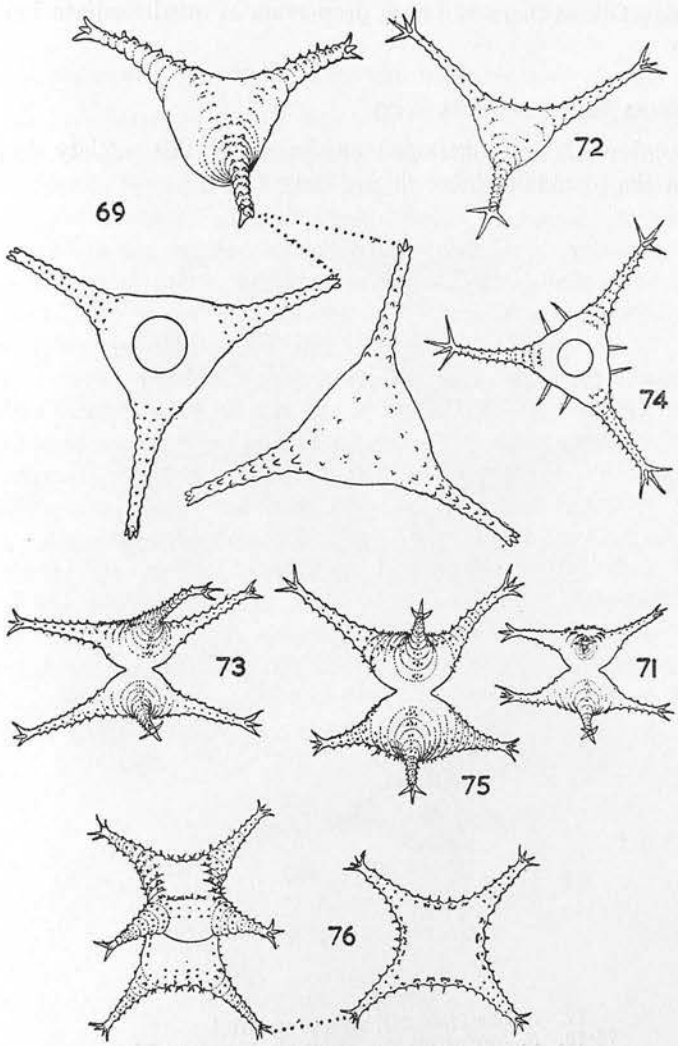
As in the case of the ornamentation of all desmid species, that of *S. dorsidentiferum* varies considerably in prominence, and though no specimens have been seen in the present samples in which this has been reduced to the extent indicated in the West's original description, a few have been observed in which all decoration except the dorsal row of enlarged spines has been somewhat difficult to discern (fig. 69). In a few specimens even the dorsal spines were much reduced in size.

Many features of the species indicate its affinity with the *manfeldtii-sebaldi* group of *Staurastrum* (compare figs. 68 and 69 with text fig. 70,



66. *S. sebaldi* var. *ornatum* fa *planctonicum* Teiling
67. *S. planctonicum* var. *bulbosum* Teiling (?)
68. *S. dorsidentiferum* West and West
70. *S. sebaldi* var. *ornatum* Nordst. forma

a large specimen of *S. sebaldi* var. *ornatum* from Lough Corrib). Especially important in this respect is the enlargement and forward protrusion of the inner (lower) terminal teeth of the processes. This seems to be a very constant character for all members of this species group.



69. *S. dorsidentiferum* West and West
72–76. *S. anatinum* Cooke and Wills, various forms

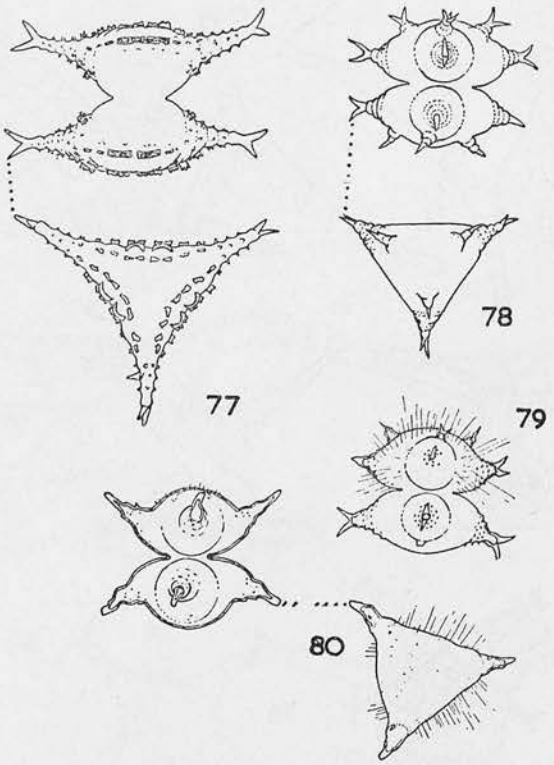
S. anatinum Cooke and Wills

A number of forms of this very variable species have been found in the present collections. These include small forms with little ornamentation apart from their typical apical verrucae (fig. 71). Some forms

have long, slender, denticulate processes which could be referred to the var. *longibrachiatum* West and West (figs. 72–73); others in all respects identical with the latter but much more conspicuously ornamented, many bearing lateral spines or verrucae on the semicell body (fig. 74), must be referred to the species *S. vestitum* Ralfs. Some very robust forms, also with *vestitum* characters have been found in Lough Beltra (fig. 75) and amongst these there is a high proportion of quadriradiate individuals (fig. 76).

S. anatinum var. *truncatum* West

A number of well developed specimens of this variety have been found in the plankton of Lough Ardderry (fig. 77).



77. *S. anatinum* var. *truncatum* West
78–79. *S. furcigerum* var. *reductum* West and West
80. *S. furcigerum* var. *simplicissum* nov. var.

S. furcigerum Bréb

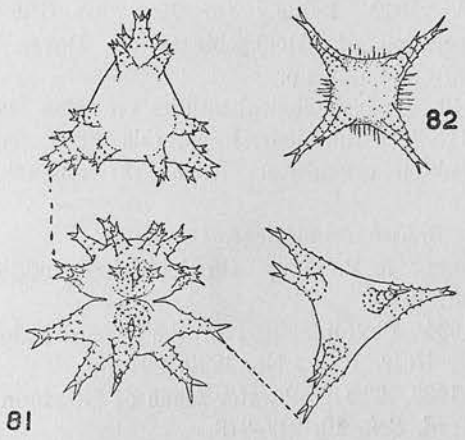
An unusual specimen of this desmid has been found in Lough Bofin (fig. 81). In this, one semicell is typical of the type species with its apex bearing well developed processes within each angle (lower semicell in fig. 81). The other semicell, however, strongly resembles the forma

eustephana (Ehr.) Nordst. in that the apical whorl of processes is doubled, consisting of 6 instead of 3 processes as in the normal triradiate specimens. In addition, on each side of the lower processes were developed small, bifurcate accessory processes having a marked resemblance to those found on *S. arcuatum* var. *senarium* Grönbl. or *S. subavicula* var. *nigrae-silvae* (Schmidle) Grönbl. A quadriradiate form of *S. furcigerum* has also been found in L. Bofin (fig. 82).

S. furcigerum var. *reductum* West and West

It is of interest to record that this variety, which is distinguished by the great reduction of the superior (apical) processes, still persists in Lough Corrib, from where it was originally described by the Wests more than 50 years ago (West and West, 1906). Frequently specimens have been found in the present collection from this lough in which the upper and lower processes were tipped with only one stout spine instead of the normal two (fig. 78). In others there may be a complete suppression of the upper processes (see lower semicell in fig. 79).

Some forms which are also quite frequent in Lough Corrib, show a complete reduction of all the upper (apical) processes while in each of the three lower processes only a single hollow spine remains in place of the normal pair of divergent spines (fig. 80). Teiling (private communication), who has also recently examined material from this lough, suggests that such forms, since they are a very constant strain, are worthy of varietal distinction and proposes that they should be named var. *simplicissimum*. This name seems most appropriate since it implies the end of an evolutionary series which shows increasing reduction of the processes from the elaborate variety *armigera* (Bréb.) Nordst., through the type species, then the var. *reductum* to this newly described, simple form.



81. *S. furcigerum* Bréb., dichotypical form
82. *S. furcigerum*, facies *quadriradiata*

ACKNOWLEDGMENT

The author wishes to express his sincere thanks to Dr. Einar Teiling for his generous advice about some of the desmids dealt with above and especially for assistance with the nomenclature of the genus *Staurodesmus*.

SUMMARY

Descriptions and comments are given concerning 30 rare or unusual species or varieties of desmids found in the plankton from loughs in northern and western Ireland. Of these, *Staurastrum furcigerum* var. *simplicissimum* from Lough Corrib is new to science, while *S. ornatum*, *S. pingue*, *S. chaetoceras*, *S. cingulum* var. *obesum*, *S. sebaldi* var. *ornatum* f. *planctonicum* and *Staurodesmus joshuae* do not seem to have been previously recorded from the British Isles. *Micrasterias conferta*, *Cosmarium pseudoprotuberans*, *C. alpestre* and *Staurastrum boreale* have not been recorded before from Ireland.

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